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Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

100th Anniversary

100e anniversaire

http://www.nrc.ca/cisti/journals

ISSN 0706-652X / CJFSDX 58(7) 1261–1487 (2001)

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Volume 58, Number 7, July 2001

Canadian Journal of Fisheries and Aquatic Sciences

Published by the National Research Council of Canada

Volume 58, numéro 7, juillet 2001

Journal canadien des sciences halieutiques et aquatiques

Publié par le Conseil national de recherches du Canada

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RAPID COMMUNICATION / COMMUNICATION RAPIDE

Establishment of two invasive crustaceans (Copepoda: Harpacticoida) in the nearshore sands of Lake Michigan

Thomas G. Horvath, Richard L. Whitman, and Laurel L. Last

Abstract: Benthic copepods (Copepoda: Harpacticoida) in the nearshore sediments of southern Lake Michigan appear to be dominated by two new invasive species. We report the first occurrence in North America of *Schizopera borutzkyi* Montschenko, a native to the Danube River delta, and *Heteropsyllus* nr. *nunni*, likely a new species that is morphologically similar to the marine species *Heteropsyllus nunni* and represents the first occurrence of this genus in freshwater. *Schizopera borutzkyi* is a euryhaline species occurring in shallow sands in its native habitat and in deeper sands (6–15 m) in southern Lake Michigan. Based on the absence of these species from previous studies, we suggest that they are recent introductions. *Heteropsyllus* nr. *nunni* dominated (55–100%) the harpacticoid abundance to depths of 9 m, but *S. borutzkyi* comprised 75% of the harpacticoid abundance at 15 m. Native harpacticoids were always greatly outnumbered by invasive harpacticoids in our samples, which suggests that the natives are being replaced rapidly or that the invasive species are finding unused resources. The ecological implications of these introductions are not known, but these invasions may represent continued "invasional meltdown" in Lake Michigan.

Résumé : Le peuplement des copépodes benthiques (Copepoda: Harpacticoida) des sédiments le long de la rive sud du lac Michigan semble être dominé par deux espèces envahissantes. C'est la première fois que la présence de *Schizopera borutzkyi* Montschenko, une espèce originaire du delta du Danube, est signalée en Amérique du Nord; il en est de même pour *Heteropsyllus* près de *nunni*, probablement une espèce nouvelle morphologiquement semblable à l'espèce marine *Heteropsyllus nunni*, ce qui représente la première découverte du genre en eau douce. *Schizopera borutzkyi* est une espèce euryhaline qui vit dans les fonds sablonneux en eau peu profonde dans son milieu d'origine et dans les sables en eau plus profonde (6–15 m) dans le sud du lac Michigan. Absentes des études antérieures, ces espèces nous semblent être des introductions récentes. *Heteropsyllus* près de *nunni* est l'espèce dominante d'harpacticoïde (50–100% de la densité) jusqu'à une profondeur de 9 m, alors que *S. borutzkyi* représente 75% de l'abondance des harpacticoïdes à 15 m. La densité des harpacticoïdes envahissants dépasse toujours de beaucoup celle des harpacticoïdes indigènes dans nos échantillons, ce qui laisse croire que les espèces indigènes sont en train d'être remplacées rapidement ou alors que les espèces envahissantes trouvent des ressources inutilisées. Ces invasions ont des conséquences écologiques inconnues, mais elles s'insèrent peut-être dans un processus d'« effondrement » de la communauté consécutif aux invasions (« invasional meltdown ») en cours au lac Michigan.

[Traduit par la Rédaction]

Introduction

Exotic species in the Laurentian Great Lakes are becoming increasingly more common. Most introduced species are coming into the Great Lakes via ballast water, and a majority of the recent invaders have been euryhaline species originating from the Ponto–Caspian region (Ricciardi and MacIsaac 2000). Crustaceans appear successful at surviving transport in ballast water, possibly because many have mechanisms (e.g., resting eggs or encystment) to deal with periods of unfavorable environmental conditions or are able to adapt to rapid changes in salinity that occur during ballast water exchange (Lee and Bell 1999). In addition, the water bodies in the Ponto–Caspian region are particularly rich in

Received April 11, 2001. Accepted May 23, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 4, 2001. J16309

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 DOI: 10.1139/cjfas-58-7-1261 © 2001 NRC Canada

endemic species, especially crustaceans. Exotic crustaceans recently reported in the Great Lakes include the pelagic cladocerans *Cercopagis pengoi* (Ostroumov) (MacIsaac et al. 1999) and *Daphnia lumholtzi* Sars (Muzinic 2000). Changes in the pelagic crustacean community have affected ecosystem function, but the role of benthic crustaceans, especially harpacticoids, is much less known (Hudson et al. 1998), and changes in the benthic zone may have similarly important ecological effects.

In marine ecosystems, harpacticoids form an integral link in food webs by coupling nutrients with higher trophic levels, such as salmonid fish (Fujiwara and Highsmith 1997), and also structure benthic and pelagic links (Gregg and Fleeger 1998). In freshwaters, harpacticoids are major consumers of microbial carbon production and may provide an efficient pathway for energy transfer to higher trophic levels (Hudson et al. 1998). Thus, changes in the harpacticoid community may cause drastic shifts in ecosystem processes originating in or involving the benthic zone.

Materials and methods

We report changes in the meiobenthic community composition of two areas of southern Lake Michigan, which have been invaded by two harpacticoids. To document the community composition of the nearshore meiobenthos, we collected benthic samples from two sites in the nearshore sands of southern Lake Michigan: Indiana and Chicago. The Indiana site was located directly offshore from Mt. Baldy, Indiana Dunes National Lakeshore (41°42′N, 86°55′W) and was sampled on a single date in years 1996–2000 (14 August 1996, 4 December 1998, 22 October 1999, and 28 August 2000). Specific conductance in this area is around 300 $\mu S \cdot cm^{-1}$. A single ponar sample (232 cm^2) was taken at depths of 1.5, 4, and 6 m along each of four transects ($n = 4$ for all analyses) in all years except 2000, when samples were collected in triplicate along a single transect but at depths of 1, 1.5, 4, 6, 9, and 15 m. The Chicago site was sampled once on 7 December 1999 by collecting 50 ponar samples from randomly selected spots within an area between Diversey and Belmont harbors (41°56′N, 87°37′W). Depth in this area was between 2 and 5 m. Sediments generally were fine- to coarse-grained sands with very little organic matter (<1%). Organisms were elutriated by hand-swirling the sands and immediately decanting the overlying water into a 106-µm-mesh sieve; the procedure was repeated three times. Harpacticoid species were confirmed by taxonomic experts.

Results and discussion

Five species of harpacticoids were encountered in the nearshore sands of southern Lake Michigan. *Canthocamptus robertcokeri* M.S. Wilson is common to all the Laurentian Great Lakes, and densities greater than 1000 individuals·m^{-2} have been reported from southeastern Lake Michigan (Nalepa and Quigley 1985). *Epactophanes richardi* Mrazek has been reported in all the Great Lakes except Lake Superior (Hudson et al. 1998) and is a cosmopolitan species. *Nitokra hibernica* (Brady) is an exotic species apparently originating from the Ponto–Caspian region and is widely distributed throughout Europe. It was first reported in the Great Lakes in Lake Ontario but has since established in all the Great Lakes except Lake Superior (Hudson et al. 1998).

This work reports the first occurrence of *Schizopera borutzkyi* Montschenko in North America (reference specimens are kept at the Royal Belgium Institute for Natural Sciences (RBINS) Invertebrate Collection under COP 4535). We also report the occurrence of an unknown harpacticoid species in the genus *Heteropsyllus* that represents the first reported occurrence of this genus in freshwater (reference specimens are kept at the RBINS Invertebrate Collection under COP 4533). This species has yet to be described but is morphologically similar to *Heteropsyllus nunni* Coull and hereafter will be referred to as *Heteropsyllus* nr. *nunni*.

Schizopera borutzkyi belongs to the family Diosaccidae and is a speciose genus (at least 83 reported species), although none is found in North America. Very little work has been published on *Schizopera borutzkyi*; previously, it has been reported only from the Black Sea in the Danube River delta (Montschenko 1967). In its native habitat, *S. borutzkyi* is found in shallow muds and sands of the delta, where water temperature was 21°C and pH was 7.6 (Montschenko 1967). Salinity changes in the delta depending on discharge from the Danube River. *Schizopera borutzkyi* can tolerate a variety of salinities (0.04–6‰) but is most often found in areas of low salinity (Montschenko 1967). It is distinct from other common Lake Michigan harpacticoids in that it has a broad rostrum and caudal rami twice as long as wide (see Montschenko (1967) for detailed species descriptions). The typical body size of collected individuals was about 520 µm.

Heteropsyllus is a modest-sized genus (at least 13 reported species) belonging to the family Cletodidae. *Heteropsyllus* spp. are known mostly from marine coasts along northern Europe but *H. nunni* and *H. pseudonunni* are native to the North American east coast. Some striking differences are evident between *H.* nr. *nunni* in Lake Michigan and its marine congeners. In marine habitats, *Heteropsyllus* spp. tend to be winter univoltine species (e.g., *H. nunni*; Williams-Howze and Coull 1992), but we found large numbers of *H.* nr. *nunni* in July samples as well as in December samples. Most *Heteropsyllus* spp. tend to be found at depths >>10 m along European coasts, although *H. nunni* was collected from shallow sands along North American coasts (Williams-Howze and Coull 1992). We collected the highest densities of *H.* nr. *nunni* in Lake Michigan at depths around 9 m. These differences, plus subtle morphological differences (B. Coull, University of South Carolina, Columbia, SC 29208, and J. Williams, University of Southern Mississippi–Gulf Coast, Long Beach, MS 39560, personal communications), support the conclusion that *H.* nr. *nunni* is a separate species from *H. nunni*. The typical body size of collected *H.* nr. *nunni* was about 510 µm.

It is currently impossible to claim a vector of introduction for *H.* nr. *nunni* because its origins are not known. However, for a number of reasons, the most likely vector of invasion for *S. borutzkyi* into Lake Michigan is ballast water exchange. (*i*) Numerous invasion routes exist directly linking the Great Lakes with the Black Sea (Ricciardi and MacIsaac 2000). (*ii*) Ballast water has been implicated as the transport vector in most arrivals from Europe since the 1980s (e.g., *Dreissena polymorpha*, *Cercopagis pengoi*, *Gymnocephalus cernuus*; Ricciardi and MacIsaac 2000). (*iii*) Harpacticoids are known to survive long periods in ballast water (Chu et al. 1997), which would be required of a transoceanic voyage. Current ballast-water exchange programs may not have prevented *S. borutzkyi* from entering the Great Lakes because

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Fig. 1. Abundance of harpacticoids at both the Chicago and Indiana sites. Bars represent means and error bars are +1 standard error (SE) (n = 50 for Chicago site and n = 4 for Indiana site). The solid line connects the years from the Indiana site only.

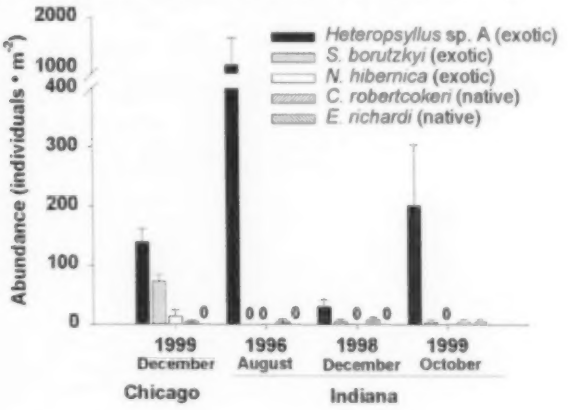
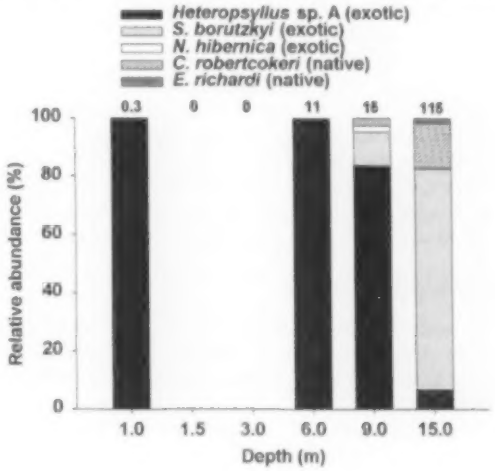


Fig. 2. Relative abundance of harpacticoid species collected on 28 August 2000 from a single transect at the Indiana site. Percentages are based on the means of three samples, and numbers above the bars are the mean number of harpacticoids collected.



its euryhaline nature (Montschenko 1967) would allow it to tolerate the salinity changes that occur during ballast-water exchange, especially if it was transported while encysted.

It was clear that the new invasive species were the numerically dominant taxa in our samples (Figs. 1 and 2). At the Chicago site, *H.* nr. *nunni* was significantly more abundant than *S. borutzkyi*, *C. robertcokeri*, and *N. hibernica* (Kruskal–Wallace test statistic = 81.462, df = 3, $p < 0.001$). Although *S. borutzkyi* was not as numerous as *H.* nr. *nunni*, it was more common than the native *C. robertcokeri* at this site in December (Fig. 1). *Schizopera borutzkyi* was absent from sediments at the Indiana site in the August 1996 samples but was collected in very low numbers in samples from 1998 and 1999, although samples were collected at different times of the year. *Heteropsyllus* nr. *nunni* was the most numerous harpacticoid at this site in 1996–1999 samples (Fig. 1), but differences in abundance among species were significant only in 1996 (Mann–Whitney U test < 0.001, df = 1, p = 0.018). In the October 2000 samples, *H.* nr. *nunni* was the most numerous harpacticoid at the shallower depths (about 550 individuals·m^{-2} between 5 and 9 m), comprising 80–100% of the harpacticoid taxa (Fig. 2). *Schizopera borutzkyi* was most numerous at the deepest site (about 3700 individuals·m^{-2} at 15 m), comprising about 75% of the harpacticoids (Fig. 2); however, it was abundant in the shallower sands at the Chicago site (72 ± 12 individuals·m^{-2}). Relative abundance of the native *C. robertcokeri* at the Indiana site increased from 2% at 9 m deep to 15% at 15 m deep.

Recent invaders?

We can not put a date of introduction on *S. borutzkyi* or *H.* nr. *nunni* because few data exist about the historical species composition of harpacticoids in the Great Lakes (see Hudson et al. 1998). We believe that *S. borutzkyi* could be a recent invader because it did not appear in our samples until 1998 and had not been collected in other intensive surveys in the Great Lakes (Evans and Stewart 1977; Nalepa and Quigley 1985; Hudson et al. 1998). The exotic *N. hibernica* was found by Hudson et al. (1998), but the harpacticoid communities generally were dominated by the commonly occurring genera *Canthocamptus* spp., *Bryocamptus* spp., and *Moraria* spp. (Hudson et al. 1998). However, Hudson et al. (1998) did not sample southern Lake Michigan, whereas Evans and Stewart (1977) and Nalepa and Quigley (1985) sampled only southeastern Lake Michigan. *Heteropsyllus* nr. *nunni* may also be a fairly recent invader for the same reason. It also was not recorded in the above-mentioned studies but has been prevalent in all of our samples beginning in 1996. However, given the high abundances of *S. borutzkyi* and *H.* nr. *nunni* relative to other harpacticoid species, we expect that they would have been collected in the other studies had they been present.

Both *S. borutzkyi* and *H.* nr. *nunni* are now common in southern Lake Michigan, but we are uncertain of their distribution beyond our sampling sites. It initially seemed that *S. borutzkyi* was not well established at the Indiana site, with only a few immature specimens collected in 1998. However, we may have missed sampling their preferred habitat in deeper areas in previous years, although they were found commonly in shallow sands at the Chicago site. *Heteropsyllus* nr. *nunni* may be more prevalent in the Great Lakes than realized; a few individuals were collected from Lake St. Clair during the summer of 2000 (P. Hudson, Great Lakes Science Center, Ann Arbor, MI 48105, personal communication). Genetic and molecular tools may give better insight into the timing of introductions and the extent to which populations have established.

Ecological implications

Our data document that *S. borutzkyi* and *H.* nr. *nunni* have become established in the nearshore habitats of southern Lake Michigan. *Heteropsyllus* nr. *nunni* is clearly the most abundant harpacticoid at shallow sites, whereas *S. borutzkyi* is the most abundant at deeper sites. The ecological implications of these invasions are unclear because little is known about the specific role of harpacticoids in the Great Lakes. It is possible that these invaders negatively affect the native

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species, if they are in direct competition for similar resources. Alternatively, the invaders may be using habitats or trophic resources not being used by the native species. We can only speculate about further changes that these invasive species may cause in the nearshore food web, but we can say with some confidence that changes are occurring in the harpacticoid community composition. These changes are similar to changes occurring in the pelagic and other benthic communities, which are experiencing increased numbers of introduced species originating from the Ponto–Caspian region. The presence of *N. hibernica* and now *S. borutzkyi*, both species originating from the Ponto–Caspian region, could be additional pieces of an "invasional meltdown" occurring in the Great Lakes (Ricciardi and MacIsaac 2000).

Acknowledgements

The authors thank Jason Butcher, Maria Goodrich, Meredith Nevers, and Ellen Oberdick for assistance in the field and laboratory and Douglas Wilcox, Martin Berg, William Perry, and an anonymous reviewer for providing critical review of the manuscript. The authors are grateful to Bruce Coull (University of South Carolina), Frank Fiers (Royal Belgium Institute for Natural Sciences), Rony Huys (The Natural History Museum, London), Janet Reid (Smithsonian Museum), and Judith Williams (Southern Mississippi University) for confirming the identifications of harpacticoids. The authors are especially grateful to Patrick Hudson (USGS, Great Lakes Science Center, Ann Arbor) for his constant assistance with harpacticoid taxonomy. This research was partially funded through grants from the U.S. Army Corps of Engineers (W81G6693165796) and through a cooperative agreement with the Chicago Department of Environment. This article is contribution 1149 of the USGS Great Lakes Science Center.

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ARTICLES

Predictions of critical habitat for five whale species in the waters of coastal British Columbia

Edward J. Gregr and Andrew W. Trites

Abstract: Whaling records from British Columbia coastal whaling stations reliably report the positions of 9592 whales killed between 1948 and 1967. We used this positional information and oceanographic data (bathymetry, temperature, and salinity) to predict critical habitat off the coast of British Columbia for sperm (*Physeter macrocephalus*), sei (*Balaenoptera borealis*), fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), and blue (*Balaenoptera musculus*) whales. We used generalized linear models at annual and monthly time scales to relate whale occurrence to six predictor variables (month, depth, slope, depth class, and sea surface temperature and salinity). The models showed critical habitat for sei, fin, and male sperm whales along the continental slope and over a large area off the northwest coast of Vancouver Island. Habitat models for blue, humpback, and female sperm whales were relatively insensitive to the predictor variables, owing partially to the smaller sample sizes for these groups. The habitat predictions lend support to recent hypotheses about sperm whale breeding off British Columbia and identify humpback whale habitat in sheltered bays and straits throughout the coast. The habitat models also provide insights about the nature of the linkages between the environment and the distribution of whales in the North Pacific Ocean.

Résumé : Les statistiques de chasse à la baleine accumulées par les stations baleinières de la côte de la Colombie-Britannique entre 1948 et 1967 indiquent de façon fiable les coordonnées géographiques des points de capture de 9 592 baleines. Ces données géographiques combinées à des informations océanographiques (bathymétrie, température et salinité) ont servi à prédire l'habitat critique des Cachalots macrocéphales (*Physeter macrocephalus*), des Rorquals boréaux (*Balaenoptera borealis*), des Rorquals communs (*Balaenoptera physalus*), des Rorquals à bosse (*Megaptera novaeangliae*) et des Rorquals bleus (*Balaenoptera musculus*) au large des côtes de la Colombie-Britannique. Des modèles linéaires généralisés à échelles annuelles et mensuelles ont permis de mettre en correspondance la présence des baleines et six variables prédictives (mois, profondeur, pente, classe de profondeur et température et salinité de surface de la mer). Les modèles ont révélé l'existence d'habitats critiques pour les Cachalots macrocéphales mâles, les Rorquals boréaux et les Rorquals communs le long du talus continental et sur une grande surface au large de la côte nord-ouest de l'île de Vancouver. En partie à cause d'un échantillonnage plus faible, les modèles d'habitat des Cachalots macrocéphales femelles, des Rorquals bleus et des Rorquals à bosse restent relativement insensibles aux variables prédictives. Ces prédictions sur les habitats viennent appuyer des hypothèses récentes qui veulent que les Cachalots macrocéphales se reproduisent au large de la côte de la Colombie-Britannique et qui indiquent que l'habitat des Rorquals à bosse se situe dans les baies et les détroits protégés tout le long de la côte. Ces modèles d'habitat laissent aussi entrevoir la nature des liens qui existent entre les conditions de l'environnement et la répartition géographique des baleines dans le Pacifique nord.

[Traduit par la Rédaction]

Introduction

Interest in the spatial distribution of whales in the world's oceans can be traced back to the Yankee sperm whaling industry and the charts of Townsend (1935) and Maury (1852). More recent efforts to relate whale distributions to oceanographic parameters can be traced to work by Uda (1954) who identified four types of oceanic fronts that were correlated with the presence of whales. This line of research culminated with Nasu (1966) who detailed the oceanographic conditions (mainly temperature and currents) that formed favourable whaling grounds in the North Pacific and described the seasonal effects of temperature and current on the distributions of blue (*Balaenoptera musculus*), fin (*Balaenoptera*

Received June 5, 2000. Accepted March 23, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 4, 2001. J15803

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 DOI: 10.1139/cjfas-58-7-1265 © 2001 NRC Canada

physalus), humpback (*Megaptera novaeangliae*), and sei (*Balaenoptera borealis*) whales. The objective of these early studies was to improve the efficiency of the whaling fleets by reducing the amount of time spent searching for whales.

Recently, geographic information systems and remote sensing data have revived interest in the search for relationships between oceanographic conditions and marine mammal distributions. For example, relationships have been detected between marine mammal abundance and bathymetry (Hui 1985; Woodley and Gaskin 1996), sea surface chlorophyll concentrations (Smith et al. 1986), sea surface temperature (Woodley and Gaskin 1996), oceanographic circulations (Waring et al. 1993; Woodley and Gaskin 1996), and prey abundance (Woodley and Gaskin 1996; Fiedler et al. 1998). However, less work has been done to quantify habitat characteristics based on these relationships (e.g., Watts and Gaskin 1985; Moses and Finn 1997).

The objective of our study was to identify coastal regions that may be regarded as critical habitat for sperm (*Physeter macrocephalus*), fin, sei, blue, and humpback whales. We considered male and female sperm whales separately because of well-documented behavioural differences between the sexes (e.g., Best 1979). We adopted Hall et al.'s (1997) definition of critical habitat as the measure of an area's ability to provide the resources necessary for the persistence of a population. Since the baleen whales are highly migratory species, critical habitat could be expected to include feeding areas as well as common migration routes.

Our approach was based on work by Jaquet et al. (1996) and Moses and Finn (1997). Jaquet et al. (1996) analysed the correlations between nineteenth century Yankee sperm whaling records and satellite observations in the tropical Pacific at spatial scales of 220–1780 km^2 and found that historic sperm whale distributions were correlated with contemporary measurements of chlorophyll concentrations and that the degree of correlation increased as the spatial scale was increased. Moses and Finn (1997) used a logistic regression model to examine the relationship between right whale distributions off the coast of Nova Scotia on a 64 km^2 grid, using concurrent measurements of oceanography (depth and surface temperature) and whale presence–absence.

We sought to define critical habitat for five species of whales along the coast of British Columbia in terms of the physical environment. We did so using general linear models to determine whether the positions of historic whale catches recorded in British Columbia from 1948 to 1967 (our dependent variable) were related to six predictor variables: depth, slope, depth class, temperature, salinity, and month. Slope and depth class were derived from bathymetry, slope was a measure of topography, and depth class divided the study area into shelf, slope, and off-shelf regions. The models predicted the probability of occurrence of each species of whales based on these variables. Model results, identifying critical habitat for large whale species in British Columbia, are discussed in terms of northeastern Pacific oceanography, whale biology, and whale behaviour.

Methods

We used the positional data recorded between 1948 and 1967 by British Columbia coastal whalers and a simple oceanographic model based on depth, temperature, and salinity to create geographic probability distributions for sei, fin, humpback, blue, and sperm whales. We divided the coastal region of British Columbia into grid cells and used Cause&Effect software (Facet Decision Systems, Inc. 1999*a*) to create a habitat model, which spatially associated the dependent and independent data for each grid cell. We then exported data sets from the habitat model for regression analysis in S-Plus (Mathsoft 1999). We incorporated the results of the regression back into the Cause&Effect habitat model for display. Positional data, recorded in latitude and longitude, were converted to a regular universal transverse mercator grid for analytical and display purposes. Universal transverse mercator grids, which are measured in metres, are the preferred representation for spatial analysis because latitude and longitude measures do not reflect consistent distance measures.

We began the analysis by exploring the relationships between the predictor variables and the probability of whale presence. We then postulated an a priori "biological" model using the exploratory results. This biological model identified the terms subsequently used in the stepwise regression to create the generalized linear models. A separate regression model was generated for each species, at annual and monthly time scales. Predictions (the probability of whales being present in any given cell) were plotted on a spatial grid for visual interpretation and tested using cross-validation techniques. We also tested the sensitivity of the predictions to the predictor variables by comparing predictions from cold years with those from warm years because the temperature and salinity predictors (1980–1998) were not concurrent with the biological data (1948–1967).

The dependent variables consisted of the position, species, and date of capture for whales killed between 1948 and 1967 as part of the British Columbia coastal whaling industry. Sex was included for sperm whales only. Coastal whaling during this period was conducted solely from Coal Harbour on the west coast of Vancouver Island (Fig. 1). The whaling data used in the regression analysis were restricted to an area within 150 nautical miles (nmi) (275 km) of the mouth of Quatsino Sound (n = 8164 whales). This is where whales were often left for pickup by shore vessels. Whales killed within the 150-nmi radius represented about 85% of the georeferenced whale kills. Choosing this restricted area increases the likelihood that the whalers searched with equal effort throughout the study area and is well within the range of the whaling vessels (approximately 200 nmi) (Pike and MacAskie 1969). Regions within the 150-nmi search area that had no recorded kills were assumed to be empty of whales. Thus, we assumed that the spatial patterns of whales killed within the study area were primarily a function of whale distributions and less a function of concentrated whaling effort. Shortcomings of this assumption and the consequences of nonrandom sampling are considered in the Discussion.

Independent variables

We used three continuous and three categorical predictor variables. The continuous variables included a 5-minute grid of bathymetry (PICES 1997) and long-term point data on surface temperature and salinity. The categorical variables consisted of month, slope, and depth class.

To maximize the spatial resolution and minimize interannual variability, the most recent 18 years (1980–1998) of conductivity (salinity), temperature, and depth point data were obtained from the Department of Fisheries and Oceans. We reduced this large, multidimensional data set (latitude, longitude, year, day, time, depth, temperature, and salinity) to mean monthly surface temperature and salinity values. For each depth profile, we used only the mean of the values in the top 1.5 m of the water column.

In addition to these three continuous predictors, we included the categorical variables month, slope, and depth class. We included

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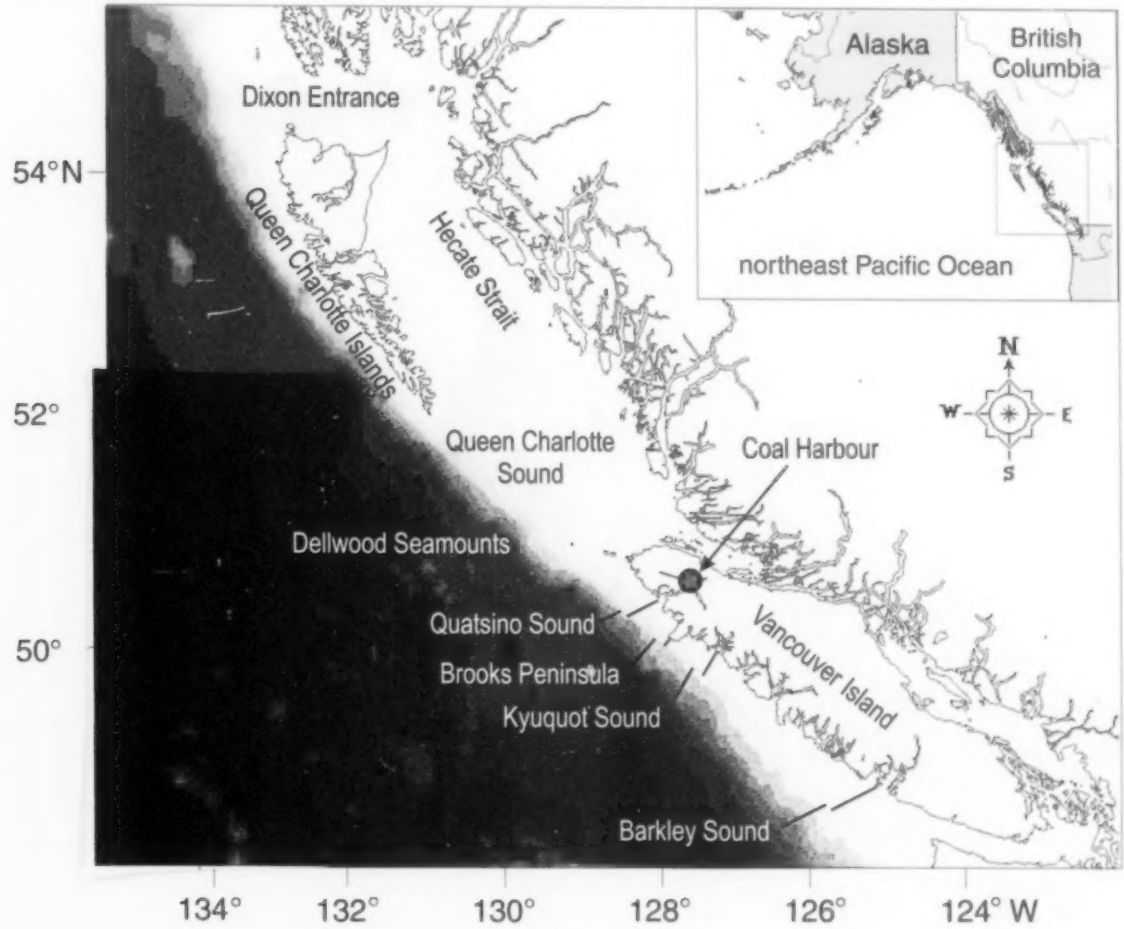
Fig. 1. British Columbia coastal waters showing the location of the Coal Harbour whaling station and other place-names mentioned in the text. Bathymetry is shaded from shallow to deep (light to dark) using 200-m bathymetric contours.



month to capture the significant species-specific monthly changes in the mean distance from shore (Gregr et al. 2000). This monthly effect (at least partially due to annual migration behaviour), combined with significant monthly changes in the temperature data (Fig. 2), shows the need to include month as a factor in the analysis. We only used the months April–September when the majority of whaling occurred (Gregr et al. 2000).

Slope was included to provide a measure of undersea topography, since topographic upwelling may play a role in biological productivity (Mann and Lazier 1996). This categorical predictor was defined to have slope classes from 0 (flat) to 6 (steepest). Although derived from the bathymetry, the slope at a particular location is independent of its depth. However, the two are strongly correlated in the area of the shelf break where there is a dramatic transition from on-shelf to deep waters.

We created the categorical predictor depth class to normalize the distribution of the depth variable, which was clearly bimodal (Fig. 3). While generalized linear models do not require the normally distributed independent variables, this does tend to yield a better fit (Tabachnik and Fidell 1996). We therefore divided the study area into three depth classes: shelf (≤200 m), slope (between 200 and 1800 m), and deep water (>1800 m). In addition to creating a more normal distribution of depths at each depth class (Fig. 3), this allowed us to capture the interaction between depth class and salinity (Fig. 2).

The study area was divided into grid cells, which thereby became the observational units in the study. We assigned annual and monthly temperature and salinity values independently to the grid cells by interpolation using triangular irregular networks (TINs) (Fig. 4). Interpolation was done equally in all directions. We did not correct for any potential spatial autocorrelation. For the annual and monthly models, we generated mean annual and monthly temperature and salinity TIN surfaces. All years were treated equally when generating the mean values, and no attempt was made to correct for the annual variance.

The bathymetric grid of point data was also mapped to the study grid using a TIN surface. The slope and depth class predictors were calculated for each grid cell after the depth was assigned. Depth class was simply a function of the depth at each cell, while slope was calculated for each cell based on the difference between the elevations of its neighbours (Facet Decision Systems, Inc. 1999*b*).

We examined the grid cells for colinearity between the assigned values using the tolerance statistic $1 - R_x^2$, where R_x^2 is the variance in each independent variable x explained by the other independent variables. A low tolerance is an indication of colinearity, with a tolerance below 0.20 considered cause for concern (Menard 1995).

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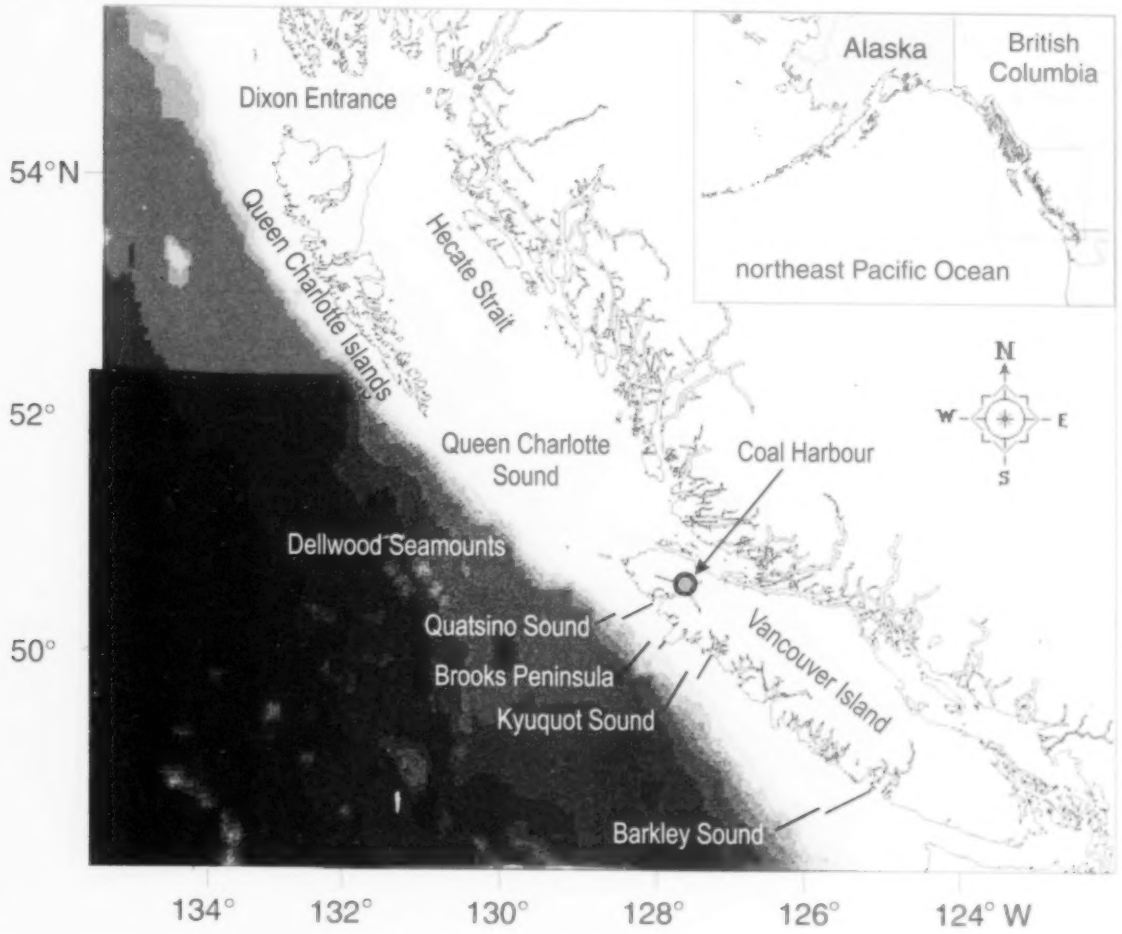

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Fig. 2. Mean effects of the categorical variables month, depth class, and slope on the distribution of the continuous predictor variables temperature and salinity for the grid cells within the 150-nmi search area (n = 9029).

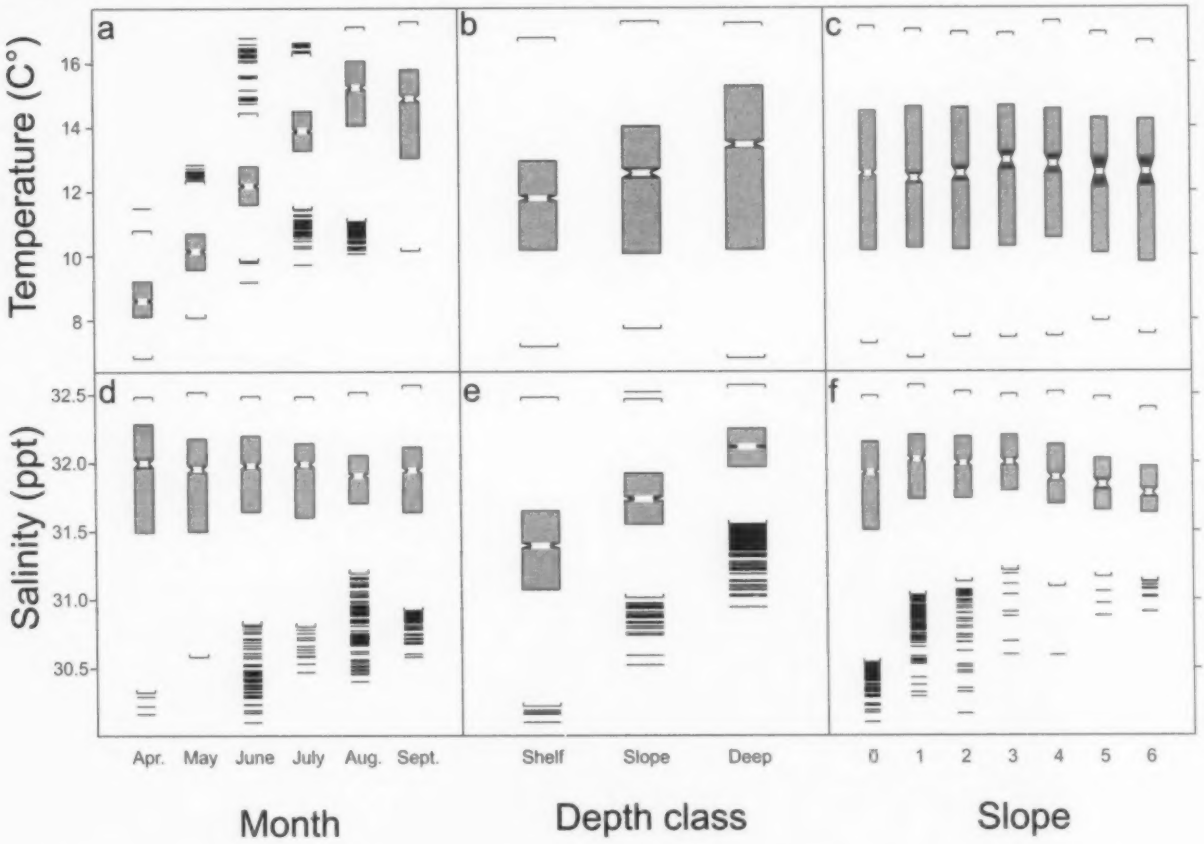
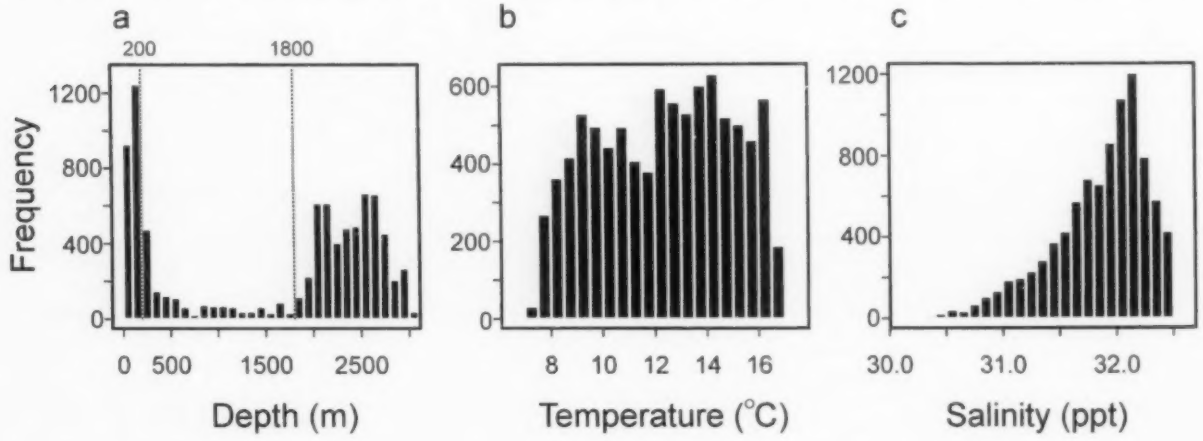


Fig. 3. Frequency distribution of the continuous predictor variables depth, temperature, and salinity for the grid cells within the 150-nmi search area (n = 9029). The vertical dashed lines on the depth–frequency plot show the three levels of the depth class categorical variable.



The tolerances for the independent variables in our study ranged from 0.47 to 0.97, indicating that the amount of colinearity was not significant at the spatial and temporal scales that we used. While some correlation between temperature and salinity might be expected, it may exist at a spatial scale (either finer or coarser) different from the one that we considered. Finally, to realistically

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bound the study area to reasonable oceanographic conditions, grid cells with depths of 10 m or less or with salinities less than 30 ppt were excluded.

Scale selection

Underlying all of the work on habitat characterization are two key assumptions. First, whales are generally found where their food is abundant, and second, these food sources are somehow related to oceanographic conditions. The relationship of common baleen whale prey species (zooplankton) to oceanographic conditions can take two forms: conditions can be ideal for primary production or oceanographic conditions can work to concentrate prey species in specific areas. In the first case, there is likely to be a temporal lag while the zooplankton blooms develop. For baleen whales feeding on zooplankton, which are trophically close to primary production (trophic levels 2.0–2.3 versus 1.0; Trites et al. 1999), this lag may be on the order of several weeks. However the lag may be considerably greater for sperm whales where the primary prey items (cephalopods, trophic level 3.7; Trites et al. 1999) are removed from primary production by approximately 4 months (Vinogradov 1981). These temporal lags typically result in corresponding spatial lags due to oceanic transport.

If the relationship between animal distributions and oceanographic predictors is more a function of prey concentration or aggregation caused by small-scale eddies or gyres, very little temporal and no spatial lag would be expected. Similarly, if certain bathymetric features (i.e., areas of high relief) caused prey species to aggregate, these lags would also be absent.

Thus, the time periods and spatial scales over which data are pooled may affect our ability to detect possible relationships between species abundance and any independent predictor variables, with different relationships or processes potentially being captured at different scales. The consequence of this fundamental scale problem was emphasized by Wiens (1989) who pointed out that just because we can provide clever explanations of the patterns that we observe, it does not necessarily follow that the patterns are anything more than artifacts of scale.

The effect of spatial scale was well treated by Jaquet et al. (1996) who demonstrated how multiscale analysis can help elucidate the effective scale of a relationship between a dependent variable and a single predictor. However, our objective was to evaluate the degree to which physical oceanography could be used to describe habitat for five different whale species. So rather than focus on a single predictor over multiple scales, we chose to examine the relationship between the catch distributions and a multivariate oceanographic model at two time scales. Using annual and monthly time scales allowed us to investigate the scale problem along an alternative axis (temporal versus spatial) and to assess the temporal variability in the habitat predictions. While multispatial scale analyses are the logical next step to explore the relationships proposed in our study, they are beyond the scope of this paper.

In selecting our spatial scale, we chose to use the finest possible resolution because fine-scale studies may be more informative than generalizations about the biological processes underlying the patterns (Wiens 1989). We selected a spatial resolution of 10 × 10 km based on an examination of the catch data, which showed that whalers tended to round their location to the nearest 5 minutes of both latitude and longitude (Gregr 2000). We therefore assumed this to be the precision of the positional data. Five minutes corresponds to approximately 10 km in these latitudes.

Regression modeling methods

Generalized linear models apply linear regression techniques to nonlinear data with heterogeneous variances (Chambers and Hastie 1993). Poisson and logistic regression are two types of generalized linear models that are used to model counts and binomial values (i.e., presence–absence), respectively. To capture the number of whales in the grid cells, we used Poisson rather than a logistic regression. Using a simple transform, we then converted the predicted number of whales (generated by the Poisson model) into probabilities. We mapped these probabilities onto the study area to generate the habitat predictions. An overview of these generalized linear modeling methods is contained in Gregr (2000). The transformation of counts into probabilities is described in the Appendix.

Model building

For each of the five species, we began with an exploratory analysis of how each of the continuous variables independently affected the presence of whales. We fit lowess (locally weighted scatterplot smoothing) curves to scatterplots showing the presence or absence of whales versus the independent variables. We examined the mean effects as well as the effects for each month and for each depth class. We used the results of this analysis to hypothesize a relationship between the presence–absence of whales and the independent variables based on biological significance. We used this a priori biological model to define the upper limit on the complexity of the regression models.

To generate the predictive models for each species, we used forward stepwise selection (Chambers and Hastie 1993). This technique repeatedly adds terms to the model from a pool of potential independent variables. The terms are added in order of the amount of variance that they explain. Thus, the most significant variables enter the model first. The pool of variables available for selection was defined by the biological model. We found that this approach consistently produced simpler models than stepwise backward elimination, which repeatedly removes terms from an overspecified model until the remaining terms are all statistically significant.

We applied forward stepwise selection to all the data within the 150-nmi search radius for each species to select the model terms. We determined the model coefficients using these same data. We then produced the habitat maps for the entire British Columbia coast from the annual and monthly probability predictions.

Model testing

We tested the predictive power of the models using cross-validation and classification tables. Cross-validation requires dividing the data into a fitting set and a testing set. The fitting set is used to fit the model (i.e., to generate equation coefficients). The fitted model is then tested against the testing data set. For each species, we used half of the grid cells within the 150-nmi search area for fitting and the other half for testing. Since the predictions generated by our models were probabilities, we used classification tables to evaluate the model fit.

Classification tables provide a measure of the efficiency of a predictive model. This predictive efficiency represents, in percent, how successfully a model predicts presence and absence. The tables compare the observed presence–absence in the testing data with predicted model values. In order to evaluate the predictive efficiency of our models, we needed to define a cutoff value that would convert probability into a presence–absence result. We set this cutoff value individually for each model such that the fitted model produced the same number of presence cells as found in the fitting data set.

To assess the effects of using mean surface temperature and salinity values from a 19-year period (1980–1998) that was not concurrent with the 20 years of whaling data (1948–1967), we conducted a simple analysis of the sensitivity of the predictions to the oceanographic model. We compared predictions obtained from warm years with predictions from the remaining years. Ware (1995) analysed the patterns in climate records from the northeast Pacific and related the warmest years in British Columbia (based on air temperature anomalies) to the El Niño – Southern Oscilla-

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Fig. 4. Example of how point data were mapped onto the study grids using TINs. (*a*) Point temperature data for July; (*b*) TIN used to interpolate temperature to unsampled areas; (*c*) temperature grid resulting from the interpolation. This process was used to produce mean monthly and annual temperature and salinity grids.

tion (ENSO) events. Four of the warmest years since 1895 were associated with strong or moderate ENSO events (1983, 1987, 1992, and 1994) (Ware 1995). We chose these four years as representative of an extreme in temperature and used them to divide the temperature and salinity predictor data into "hot" and "other" years. We then generated two sets of model coefficients and compared the predictions quantitatively using a paired sample *t* test and qualitatively by comparing actual habitat predictions.

Results

The total number of each species killed, the number within the search area, the number of grid cells at the annual and monthly scales, and the mean probabilities of finding a whale (Pr(Wh)) in a grid cell are shown in Table 1. The effect of creating the observational units (grid cells) at annual and monthly time scales from whale locations can be seen by comparing the respective mean Pr(Wh) values.

Biological model

The preliminary analysis of whale presence–absence as a function of each of the independent variables showed two types of general trends: (*i*) linear trends that were either increasing or decreasing and (*ii*) trends that peaked at particular values (Gregr 2000). We examined the first-order (mean annual) effects of all six predictors on presence–absence as well as the interactions between each of the continuous variables for each level of month and depth class because of the apparent interactions between the continuous predictors and these two categorical variables (Fig. 2). This analysis confirmed the interactions between depth class and salinity and between temperature and month.

All species were most commonly found at particular depths and salinities. The response to temperature was linear for all species except humpback whales. Significant differences observed in the mean response of male and female sperm whales to temperature and salinity supported treating the sexes of this species independently.

Based on this exploratory analysis, we constructed a biological model that encompassed all of the observed effects. We defined the logit (linear component) of this a priori biological model as

$$(1)\qquad \Pr(\mathrm{Wh}) \propto f[m + slope + zClass + z^2 + (S^2 \text{ in } zClass) + (T^2 \text{ in } m)]$$

where the probability of whale occurrence (Pr(Wh)) is only proportional to $f[]$ because $f[]$ is the logit, or linear component, of the generalized linear model, not the actual probability. Equation 1 contains all of the six predictor variables: the categorical variables month (m), *slope*, and depth class ($zClass$), the quadratic relationship in depth (z^2), and salinity (S^2) and temperature (T^2) nested in $zClass$ and m, respectively. The biological interpretation of this model is simply that whale presence is dependent in some way on the month, slope, and depth class and that there is an optimum salinity at each depth class and an optimum temperature in each month.

Model building

The regression terms, the amount of variance that each explained (R_L^2), and the degrees of freedom for the annual

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models are summarized in Table 2. In all cases, when quadratic terms entered the models, their respective linear components were included. The variable *slope* was significant for all species except blue whales. *zClass* was significant for all species except female sperm whales. Among the continuous variables, z^2 was significant for all species, S^2 was significant for fin, blue, and male sperm whales only, and T^2 was significant only for sei and male sperm whales. The total amount of variance explained (R^2_L) by the annual models ranged from a low of 0.23 (humpback whales) to a high of 0.49 (fin whales). Generally, R^2_L values were higher for the groups (sei, fin, and male sperm whales) with higher sample sizes (i.e., number of whales killed).

The monthly models (Table 3) showed a higher diversity of model terms but provided marginally lower R^2_L values than their annual counterparts. All three categorical variables were significant for all species with the exception of *zClass* for female sperm whales. For the continuous variables, z^2 was significant for all species, as was S^2, which was nested in *zClass* for both humpback and male sperm whales. T was omitted only from the female sperm whale model and was nested in m for sei and male sperm whales. The R^2_L values ranged from 0.24 (humpback whales and male sperm whales) to 0.39 (sei whales).

Model predictions

The left-hand panels of the annual predictions (Figs. 5–7) show the prediction grids, while the right-hand panels show the locations of all the catches where position was recorded. Both panels show the 150-nmi search radius, which encompasses the data used in building and fitting the models. The positions shown in the right-hand panels include the small number of records from the Kyuquot Harbour, Naden Harbour, and Rose Harbour stations, which operated prior to 1948 and where positions of kills were recorded periodically.

Annual predictions for the baleen whales (Figs. 5 and 6) show sei, fin, blue, and humpback whales occupying habitats that are increasingly on-shelf, with sei whales in the areas furthest offshore. Predictions for humpback whales are almost exclusively on the shelf, while the habitat predicted for fin whales is in between that of the sei and humpback whales. Both the sei and fin whale predictions encompass a large area that includes the shelf break and an offshore area extending from the south end of the Queen Charlotte Islands southeastward, approximately one third of the way down Vancouver Island and reaching almost 100 nmi (185 km) offshore. This "habitat patch" is also apparent in the annual blue whale prediction. The annual humpback whale prediction includes large areas of the on-shelf region from the outer coast of both Vancouver Island and the Queen Charlotte Islands to the protected waters on the inside of these islands.

The annual sperm whale predictions (Fig. 7) highlight the difference between the sexes, with the males showing a much tighter distribution along the shelf and in the same habitat patch as identified for the baleen species. The prediction for female sperm whales is much more diffuse, although a stronger signal is evident in the habitat patch described above.

The seasonal predictions (Figs. 8–12) show monthly probability plots overlaid with the monthly positional data for the species. These predictions not only contain an expected monthly effect but also generally appear to refine the annual predictions, showing that the predicted probabilities shift as a function of month. This is most apparent with fin and humpback whales (Figs. 9 and 10), which have the highest probability of being on-shelf and in sheltered waters in the middle months (June–August for humpback whales and July and August for fin whales). Both sei (Fig. 8) and fin whales show an increasing probability of occurrence in the habitat patch off Vancouver Island.

Visual inspection of the correlations between the predictions and the data for sei whales shows good correlation until August, when the model fails to capture an apparent offshore movement of sei whales. The fin whale model agrees well with kills recorded in Dixon Entrance (north of the Queen Charlotte Islands) but only predicts whales in Hecate Strait in August. The seasonal humpback whale model performs well in July and August, but the month of May is poorly represented.

Seasonal predictions show a dramatic difference between male and female sperm whales (Figs. 11 and 12). Male sperm whale distributions appear to be similar to those of the baleen species, while female probabilities are distributed much more diffusely. The seasonal model for male sperm whales captures the majority of the data points in all months. The model predicts that female sperm whales should be virtually absent after May, which does not reflect the small numbers that were killed through September.

Model testing

The predictive efficiencies of the species models were defined using classification tables. The cutoff values selected consistently generated classification tables where the number of presence cells was predicted with much less efficiency than the absences. Overall monthly predictive efficiencies ranged from 0.60 (humpback whales) to 0.82 (male sperm whales), while the overall annual efficiencies ranged from 0.58 (blue whales) to 0.79 (fin whales).

For each group, we also compared the annual probability distributions generated by the "hot" (1983, 1987, 1992, 1994) and "other" predictor sets using a paired two-sample t test (Zar 1996). The resulting predictions were significantly different ($p < 0.0001$) in all cases. However, a qualitative comparison of the probability plots generated by annual models based on the "hot" and "other" data sets showed little apparent difference (Gregr 2000).

Discussion

The annual models predicted that fin, sei, and male sperm whales occurred, with near certainty, sometime over the course of the summer along the entire shelf break and in a large area extending 75–100 km beyond the shelf at the north end of Vancouver Island. This offshore region stretches from the continental shelf to approximately 100 nmi offshore and ranges from Kyuquot Sound, just south of Brooks Peninsula, to the northwest as far as the Dellwood Seamounts. Both the annual and the monthly models predicted a high probability of sei, fin, blue, and male sperm whales in this habitat patch, with lower predicted use in this area by humpback and female sperm whales. The monthly models served to capture some of

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Table 1. Comparison of sample sizes and probability of whale occurrence (Pr(Wh)) for each species at annual and monthly time scales.

	Number of whales		Annual (total grid cells = 1507)		Monthly (total grid cells = 9029)	
Species	Total	Within 150 nmi	Presence cells	Mean Pr(Wh)	Presence cells	Mean Pr(Wh)
Sei	2716	2560	574	0.38	1004	0.11
Fin	3233	2613	680	0.45	1409	0.16
Humpback	598	433	212	0.14	288	0.03
Blue	249	146	118	0.08	138	0.02
Male sperm		1800	522	0.35	909	0.10
Female sperm		612	234	0.16	263	0.03

Note: Pr(Wh) is the mean probability of finding a whale in a grid cell. Pr(Wh) reflects the proportion of grid cells that contained whale kills. Monthly grid cells were created by extending the study grid across six months (May–October). Cells where depth was >10 m and salinity <30.0 ppt were removed. Whales were distributed by month and location of capture. The coefficients for the regression equations are shown in the Appendix.

Table 2. Annual regression models showing model terms (selected using stepwise forward regression), total variance explained (R^2_L), and degrees of freedom.

Species	Model					R^2_L	df
Sei	*slope*	+ *zClass*	+ z + z^2	+ T + T^2		0.48	1495
	0.021	0.275	0.182	0.005			
Fin	*slope*	+ *zClass*	+ z + z^2		+ S + S^2	0.49	1495
	0.027	0.147	0.284		0.029		
Humpback	*slope*	+ *zClass*	+ z + z^2			0.23	1497
	0.104	0.040	0.081				
Blue		+ *zClass*	+ z + z^2		+ S + S^2	0.25	1501
		0.098	0.128		0.026		
Male sperm	*slope*	+ *zClass*	+ z + z^2	+ T + T^2	+ S + S^2	0.38	1493
	0.172	0.084	0.097	0.008	0.020		
Female sperm	*slope*		+ z + z^2			0.25	1499
	0.010		0.235				

Note: The contribution of the terms to the R^2_L is shown below each term. Degrees of freedom are based on the number of grid cells in the analysis (n = 1507) and are uncorrected for spatial autocorrelation. The coefficients for the regression equations are shown in the Appendix.

Table 3. Monthly regression models showing model terms (selected using stepwise forward regression), total variance explained (R^2_L), and degrees of freedom.

Species	Model						R^2_L	df
Sei	m	+ *slope*	+ *zClass*	+ z + z^2	+ m/T	+ S + S^2	0.39	9006
	0.116	0.012	0.147	0.098	0.009	0.010		
Fin	m	+ *slope*	+ *zClass*	+ z + z^2	+ T	+ S + S^2	0.39	9011
	0.025	0.016	0.085	0.162	0.002	0.011		
Humpback	m	+ *slope*	+ *zClass*	+ z + z^2	+ T	+ *zClass*/(S + S^2)	0.24	9007
	0.058	0.064	0.025	0.012	0.046	0.031		
Male sperm	m	+ *slope*	+ *zClass*	+ z + z^2	+ m/T	+ *zClass*/S	0.24	9005
	0.004	0.098	0.048	0.055	0.004	0.032		
Female sperm	m	*slope*		+ z + z^2		S	0.30	9015
	0.165	0.006		0.132		0.001		

Note: The contribution of the terms to the R^2_L is shown below each term. A slash denotes an interaction between categorical and continuous predictors. Degrees of freedom are based on the number of grid cells in the analysis (n = 9029) and are uncorrected for spatial or temporal autocorrelation.

the migratory movement of these species and provided predictions of seasonal peaks. Humpback and male sperm whales had the most complicated models at both annual and monthly time scales.

The apparent importance of the shelf break and the habitat patch was persistent at both the annual and the monthly time scales. The increased predicted probability in the southwest corner of the study area corresponds to a group of seamounts

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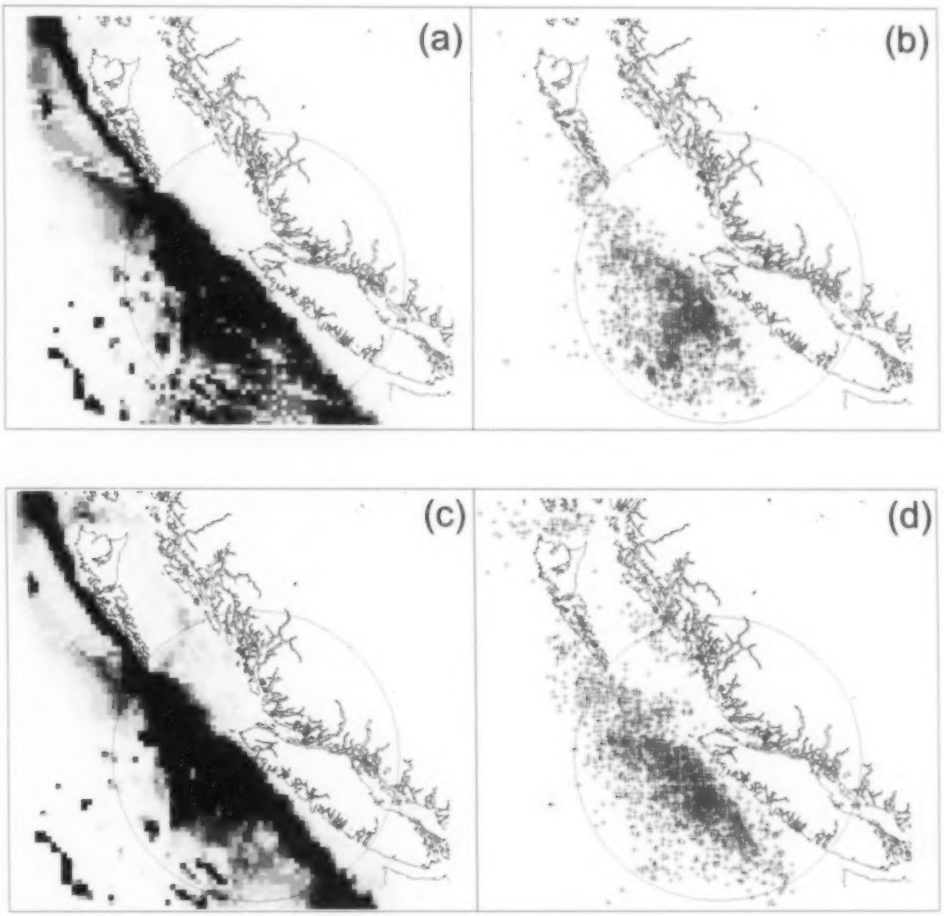
Fig. 5. Annual probability predictions and kill locations for (*a* and *b*) sei whales (n = 2716) and (*c* and *d*) fin whales (n = 3233). Dark areas represent a high probability of whale occurrence and white areas represent a low probability. The circle shows the 150-nmi (275-km) search area used to select the data for the regression analysis.



well offshore and is largely a function of the depth and slope predictors. These results support the trends observed in the preliminary analysis, confirming that in almost all cases, each of the six predictor variables played some role in defining the probability distribution of these species.

A number of the predictors that we used have been examined in previous studies, and the results are broadly similar. Bottom floor topography appears to be correlated with odontocetes (Hui 1985; Tynan 1996) and fin whales (Woodley and Gaskin 1996), while depth and temperature have been used as predictors of right whale distributions (Moses and Finn 1997). Temperature has also been cited as affecting the distribution of baleen species (Nasu 1966; Woodley and Gaskin 1996) and sperm whales (Smith and Whitehead 1993). However, the majority of work relates cetacean distributions to chlorophyll concentrations (i.e., Smith et al. 1986; Jaquet et al. 1996). Given that the relative importance of the predictors to each species is complicated by scale and by the building of the predictive models, a detailed interpretation of these results is beyond the scope of this paper. Further discussion is limited to the predictive power of our models and to the broad ecological implications of our predictions.

Sei whales

The annual model predicted a high probability for sei whales to be in deep water, while the monthly model showed strong seasonal effects. This is supported by the significant effects of depth class and month on the presence–absence of this species. The large amount of variance explained by the sei whale model suggests that this species may be closely tied to oceanographic conditions.

Fin whales

The annual habitat prediction for fin whales is consistent with Pike and MacAskie's (1969) observation that this species occurred mostly offshore but frequently entered exposed coastal seas such as Hecate Strait and Queen Charlotte Sound. The monthly predictions show how the movement of fin whales into these coastal seas is a seasonal effect (strongest in July and August). These monthly predictions support

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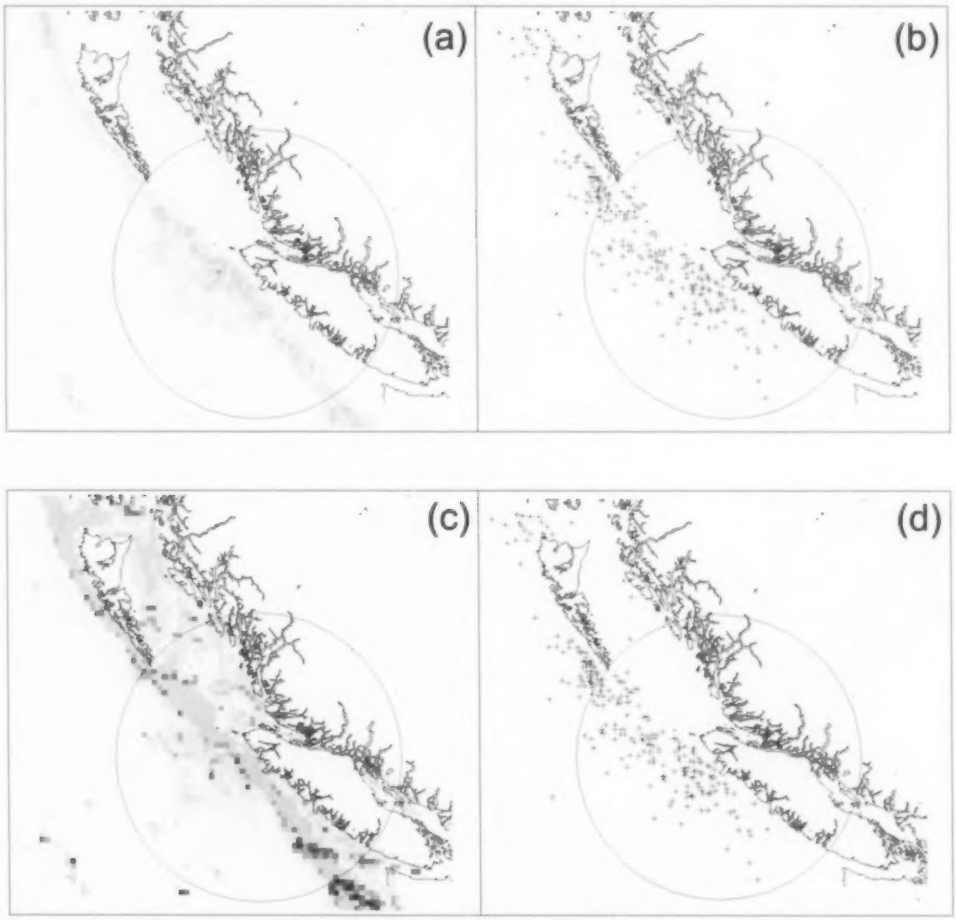
Fig. 6. Annual probability predictions and kill locations for (*a* and *b*) blue whales (n = 249) and (*c* and *d*) humpback whales (n = 598). Dark areas represent a high probability of whale occurrence and white areas represent a low probability. The circle shows the 150-nmi (275-km) search area used to select the data for the regression analysis.



the interpretation that fin whales returned to feeding grounds off the British Columbia coast (Gregr et al. 2000). The amount of variance explained rivals that of the sei whale models, implying that the historic distributions of fin whales also had a close relationship with the predictor variables. The similarity in monthly predictions between the fin and sei whale models suggests that these two species respond in a similar way to the predictor variables. However, the inability of the monthly fin whale model to capture much of the on-shelf data suggests that either the contribution of the individual predictors is unequal or a significant predictor is missing from the model.

Humpback whales

The strong affinity of humpback whales for coastal waters is confirmed by the annual model. The model predictions are consistent with reports of humpback whales in the Strait of Georgia and Barkley Sound (Webb 1988) and show a high probability of humpback whales being over the entire shelf area, including enclosed straits and inlets.

The strong interaction between depth class and salinity could be interpreted as a change in the behaviour of these animals as they move from deep water (migration), where they are relatively indifferent to salinity, to slope and shelf areas (feeding), where higher salinity may be an indication of prey abundance.

The humpback whale models (annual and monthly) explain less variance than the sei or fin whale models. This is also evident from the probability plots, which show lower probabilities for humpback whales. The low correlation coefficients of these humpback whale models are due in part to the small sample of whales killed and the partitioning of this sample into a monthly time scale. However, it may also imply that the association with the predictor variables is relatively weak and that other factors are better predictors of humpback whale habitat.

Blue whales

Given the small sample size available for this species, it is not surprising that the annual prediction shows little contrast. However, the fact that the model predicts blue whale use of the same habitat patch as sei and fin whales may be

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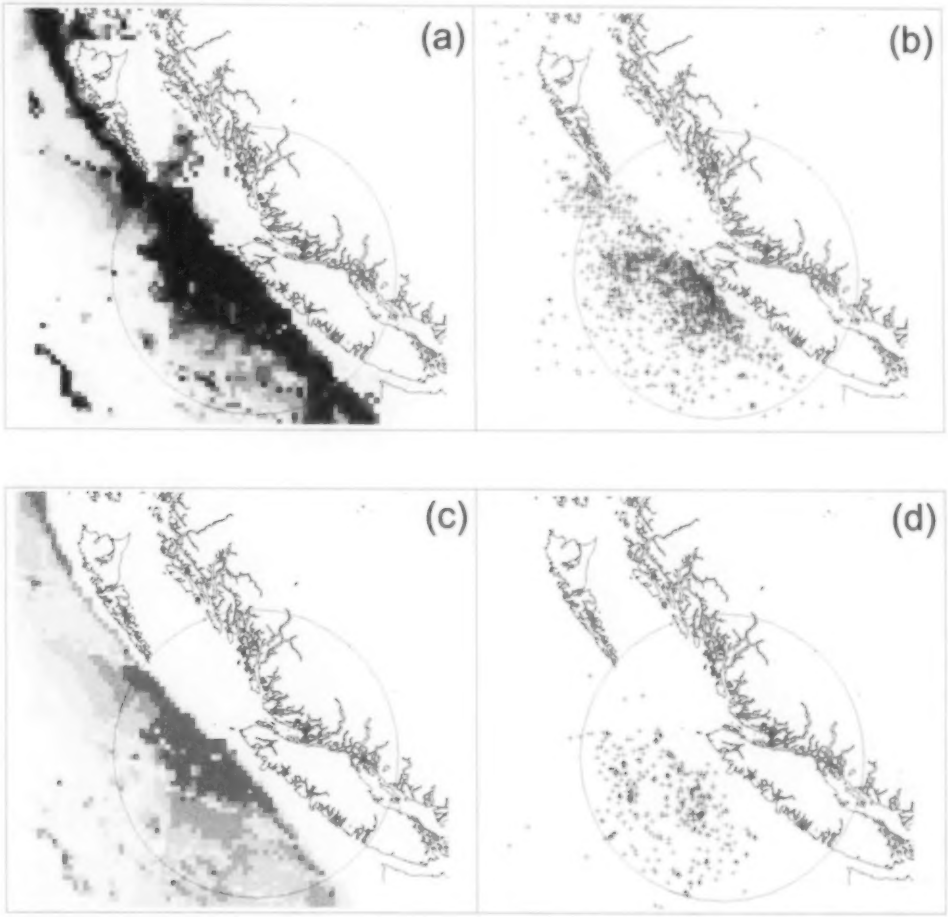
Fig. 7. Annual probability predictions and kill locations for (*a* and *b*) male sperm whales (n = 1800) and (*c* and *d*) female sperm whales (n = 612). Dark areas represent a high probability of whale occurrence and white areas represent a low probability. The circle shows the 150-nmi (275-km) search area used to select the data for the regression analysis.



significant. Given that blue whales are believed to migrate away from coastlines (Mizroch et al. 1984) and feed in eastern Pacific coastal areas (Fiedler et al. 1998), it is possible that the smaller, younger blue whales that dominated the Coal Harbour catch (Gregr et al. 2000) frequented the habitat patch off northern Vancouver Island. This is indirectly supported by our preliminary analysis, which showed the mean depth for this species to be less than that observed for the fin and sei whales.

Sperm whales

The annual model predicted a narrower distribution for male sperm whales than for the baleen species and one that is more closely associated with the shelf break. This is consistent with the strong correlation between slope and male sperm whale presence. An apparent month effect on the preferred depth of male sperm whales shows movement into shallower water after May. This is supported by the spatial shift evident in the monthly probability plot.

The annual probability plot for female sperm whales predicts a virtually uniform distribution throughout the deeper waters, although the habitat patch is shown with a slightly higher probability. The monthly predictions serve only to distribute this annual prediction between April and May. This is consistent with the observed effects of depth class and month on the presence of female sperm whales. The lack of temperature and salinity predictors in the annual model and the inclusion of a simple, linear salinity component in the monthly model explain why there is little variance in the predictions. The fact that the monthly female sperm whale model, fitted with a sample one third the size of the male model, explained more of the variance than did the monthly male model (0.30 versus 0.24) is likely due to the limited temporal distribution of female catches.

The model suggests that female sperm whales were relatively uninterested in their surrounding oceanography and supports the hypothesis proposed in Gregr et al. (2000) that sperm whale mating occurred in British Columbia waters during April and May. Given that males are spatially segregated by size, with larger males at higher latitudes (Best 1979), a reasonable hypothesis is that breeding schools travel north to increase their encounter rates with stronger,

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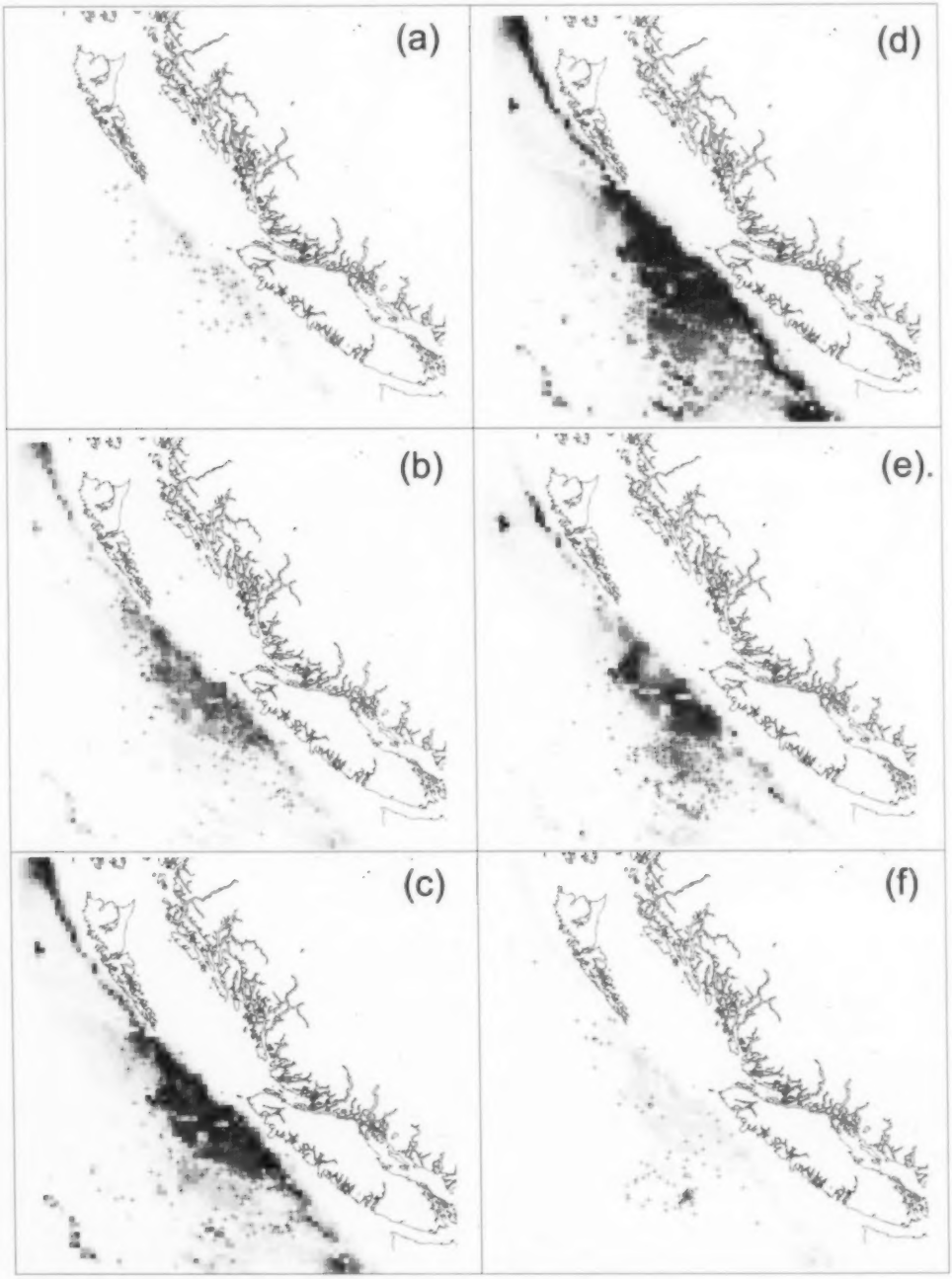
Fig. 8. Sei whale monthly probability predictions overlaid with the positions of whale kills: (*a*) April (n = 67); (*b*) May (359); (*c*) June (613); (*d*) July (1056); (*e*) August (495); (*f*) September (126). Dark areas represent a high probability of whale occurrence and white areas represent a low probability.



more mature males. Alternatively, given that the waters off Vancouver Island represent the northern boundary for female sperm whales (Reeves and Whitehead 1997), which apparently exhibit a strong degree of natal philopatry (Lyrholm 1998), this area may represent the breeding ground for a subpopulation of females. This mating hypothesis would help explain the presence of small numbers of females in the catch during all months.

Underlying processes

The processes responsible for the patterns that we observed are likely a function of oceanographic effects, which

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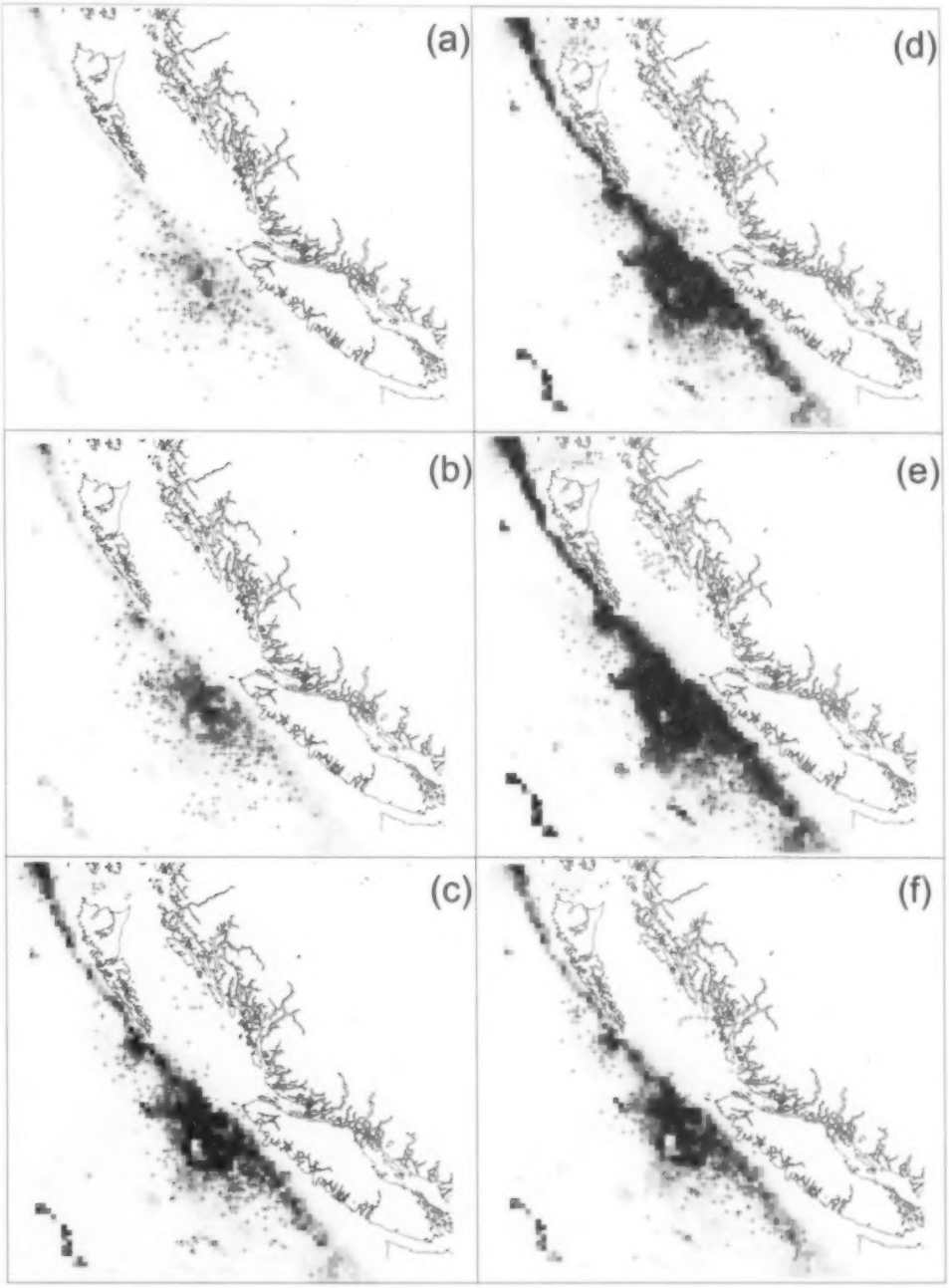
Fig. 9. Fin whale monthly probability predictions overlaid with the positions of whale kills: (*a*) April (n = 244); (*b*) May (404); (*c*) June (620); (*d*) July (727); (*e*) August (828); (*f*) September (410). Dark areas represent a high probability of whale occurrence and white areas represent a low probability.



result in enhanced productivity and (or) entrainment of prey, primarily zooplankton. Given the temporal (and spatial) lags between primary production and the development of grazing zooplankton populations, conditions that concentrate plankton may create a more suitable whale habitat than conditions that promote plankton growth.

A number of currents converge at the north end of Vancouver Island, including the Vancouver Island Coastal Current, which brings nutrient-rich, upwelled waters to the region from the southeast (Thomson 1981). This region is a highly productive area during the summer months and supports well-nourished resident zooplankton populations from spring through the fall (Mackas and Galbraith 1992). Summer circulations appear to cause a high washout rate of sur-

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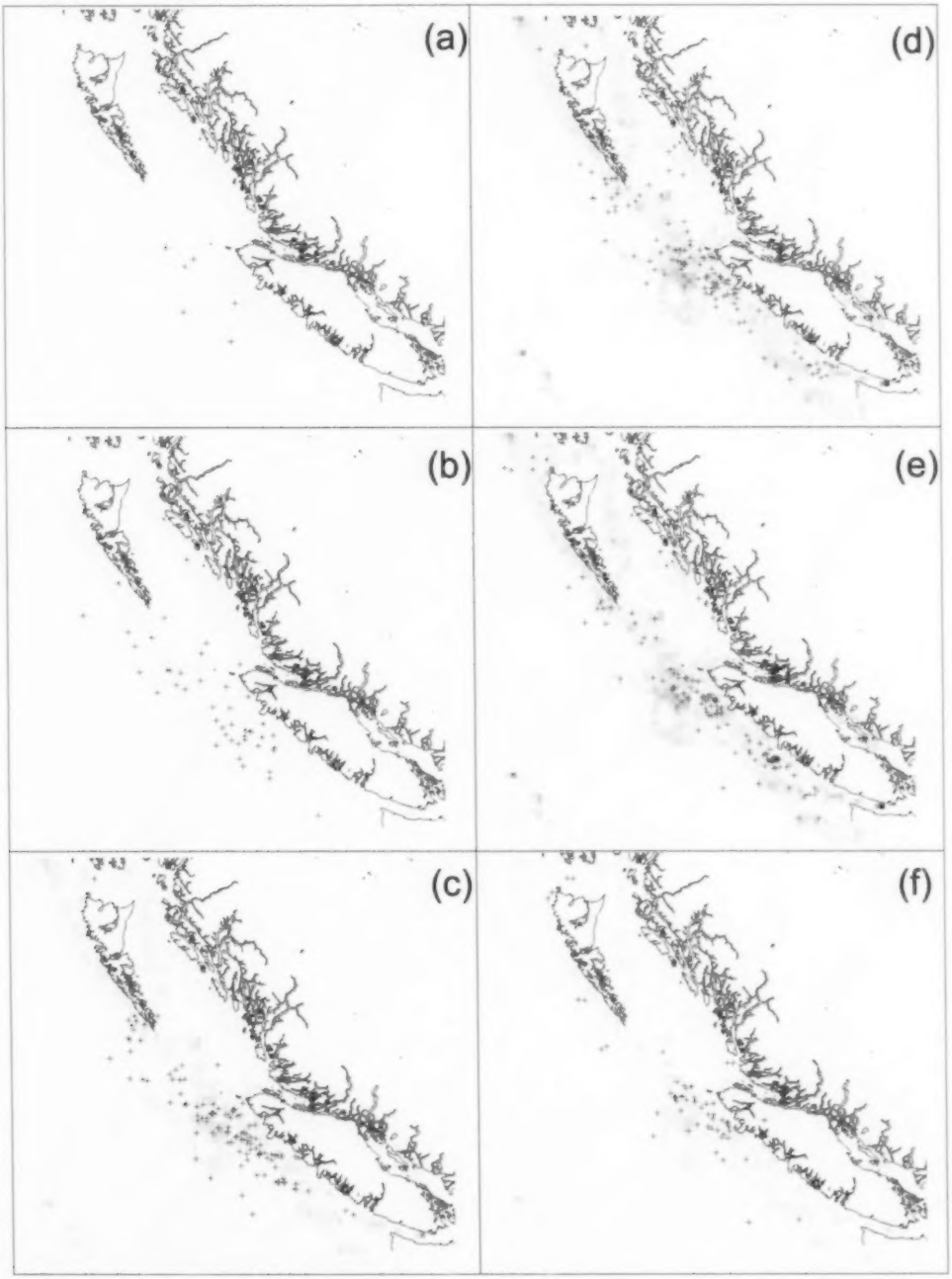
Fig. 10. Humpback whale monthly probability predictions overlaid with the positions of whale kills: (*a*) April (n = 6); (*b*) May (54); (*c*) June (133); (*d*) July (162); (*e*) August (170); (*f*) September (73). Dark areas represent a high probability of whale occurrence and white areas represent a low probability.



face zooplankton from on-shelf waters into offshore areas (Mackas 1992), where summer circulations are variable due to the bifurcation of the Kuroshio Current into the Alaskan and Californian currents (Thomson 1981). Thus, oceanographic conditions may combine to create an environment where nearshore primary production is translated into zooplankton concentrations offshore. The habitats identified by our study may be characterized by mesoscale fronts and eddies, produced by a number of converging currents, entraining both primary production and zooplankton.

The distributions of sperm whales, which feed primarily on cephalopods (Kawakami 1980), are unlikely to be influenced by the distribution of zooplankton. Rather, the data suggest that male sperm whale occurence is more closely re-

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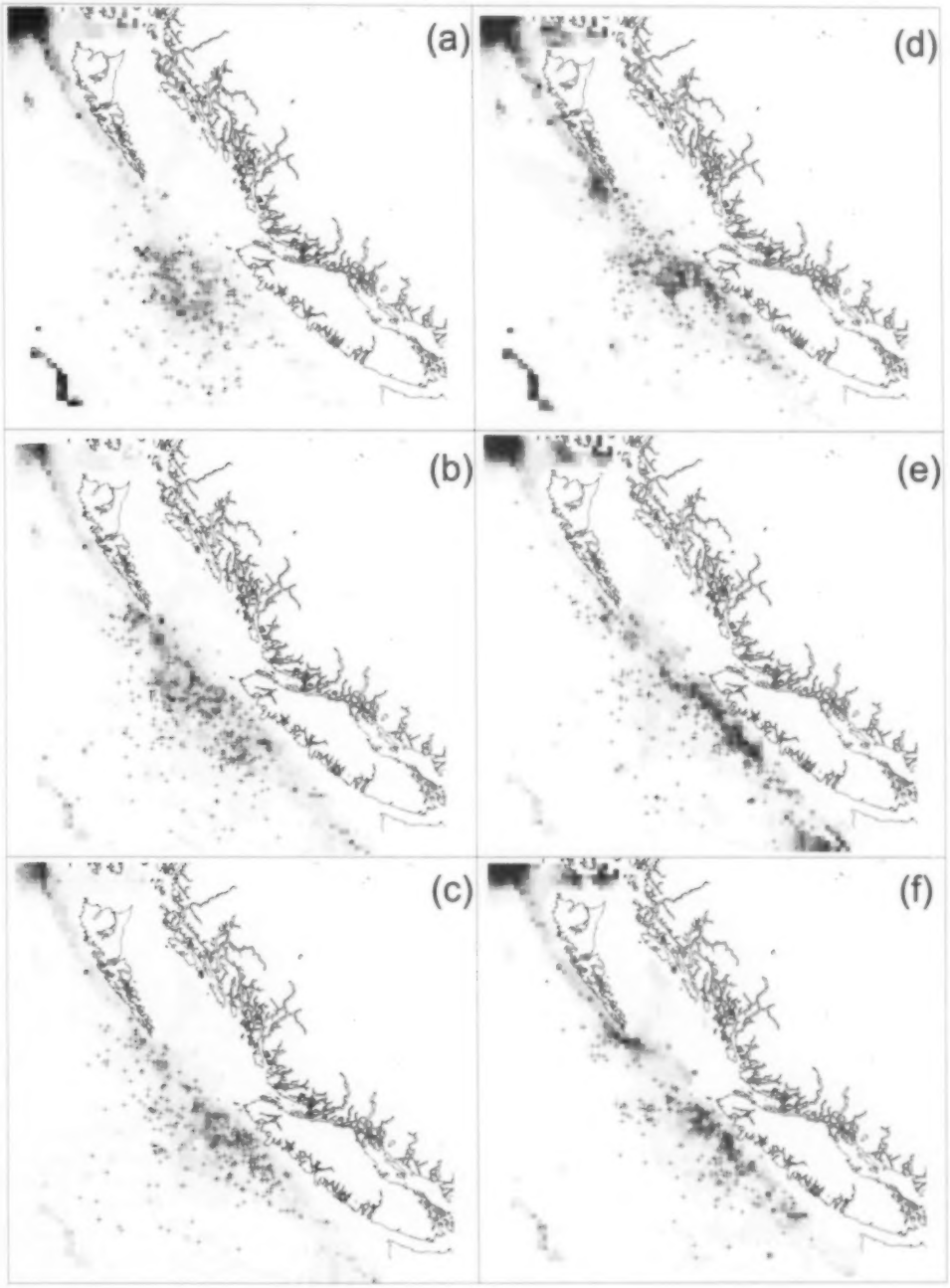
Fig. 11. Male sperm whale monthly probability predictions overlaid with the positions of whale kills: (*a*) April (n = 226); (*b*) May (402); (*c*) June (363); (*d*) July (388); (*e*) August (438); (*f*) September (340). Dark areas represent a high probability of whale occurrence and white areas represent a low probability.



lated to depth and slope. Sperm whale associations with bottom topography have also been observed in the tropical Pacific (Jaquet and Whitehead 1999) and in the northeast Atlantic (Whitehead et al. 1992). The habitat patch proposed off northern Vancouver Island overlays the Dellwood Seamounts, a region of high relief. This would explain why the critical habitat predicted for male sperm whales overlaps with that predicted for the baleen species.

Model test results

Predictive efficiencies, calculated using classification tables, are most commonly applied to dependent data that have

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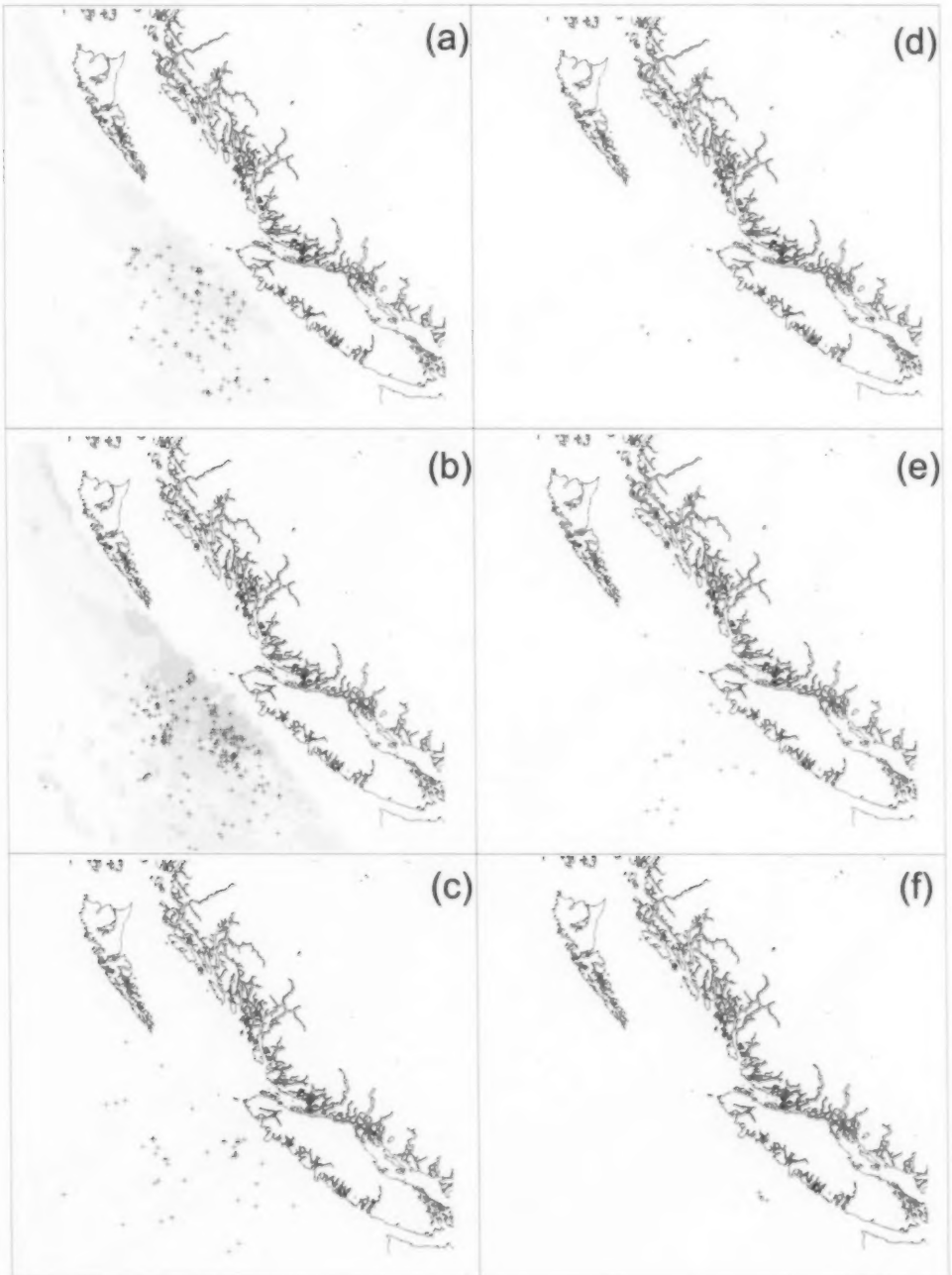
Fig. 12. Female sperm whale monthly probability predictions overlaid with the positions of whale kills: (*a*) April (n = 186); (*b*) May (328); (*c*) June (88); (*d*) July (12); (*e*) August (21); (*f*) September (4). Dark areas represent a high probability of whale occurrence and white areas represent a low probability.



no spatial component (i.e., probability of disease, probability of failure, etc.). Although we are unaware of anyone using this method to evaluate dependent data with spatial characteristics, we are also unaware of any more suitable tests of spatial predictions. Experimenting with different values for the cutoff (i.e., the value that classified a prediction as a positive or a negative outcome) showed that the calculated predictive efficiency was highly sensitive to this value. The classification tables were also sensitive to the spatial distribution of the data, since the "presence" cells were highly autocorrelated. Therefore, the composition of the (randomly generated) prediction and testing samples strongly affected

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the results. These results highlight the need for spatially explicit quantitative methods to test the spatial predictions of this and other models of habitat.

The sensitivity of our model predictions to the oceanographic data showed that while the different predictor data sets (i.e., all, hot, and other) generated statistically different predictions, the resulting probability plots were almost identical. This can be interpreted in a number of ways.

The simplest explanation is that the sample size (19 375 grid cells) is so large that any small differences between the two predictions would be statistically significant. The validity of the test is also a concern, since the grid cells are likely autocorrelated, violating a key assumption of the *t* test. This highlights the need for more sophisticated statistical methods and procedures to ensure that statistical methods are correctly applied and that spurious statistical significance is not interpreted as biological significance.

However, if we assume that El Niño events do change the spatial location of critical habitats, it may be that the relationships represented by our habitat models do not accurately capture the response to variations in temperature. It may also be that our study is at the wrong spatial scale to detect a shift in habitat as a function of these predictors. A more detailed oceanographic model, perhaps containing depth profiles, combined with concurrent biological data, would address this and other similar questions about the relative importance of all of the predictor variables.

Model biases

The habitat probability plots depict the combination of predictors that best describe where the whales were found within the study area. These "oceanographic recipes" can be considered descriptions of suitable, or perhaps even critical, habitat for these species. However, a number of complicating factors — specifically, data independence, whaling effort, TIN interpolation, and the lack of concurrency between the dependent and independent variables — must be considered when interpreting the habitat plots.

Data independence

Although we did not directly address the issues of autocorrelation (the dependence of a particular measurement on its immediate neighbors, either in space or in time) or colinearity (the effects of one variable on another), the consequences of these effects for our analysis should be considered. Autocorrelation in the dependent data can be assumed to exist at both very fine and very coarse space–time scales due to certain accepted behaviour patterns. For example, the well-documented migration of baleen species implies temporal autocorrelation at monthly time scales and spatial autocorrelation at scales on the order of hundreds or even thousands of kilometres. Similarly, the congregation of whales in areas of high food abundance implies strong spatial and temporal autocorrelation on a scale of metres and minutes. Autocorrelation at these finer scales is further implied for all species in our study by the biological data, which provide numerous examples of multiple kills of a particular species at the same time and location. Thus, the commonly asked question about point data, whether or not the observed distribution patterns are random, is of little interest in our case. Rather, the two questions that need answering are at what temporal and spatial scales are whales correlated and what are the processes responsible? While we do not attempt to answer the first question, the question of processes is central to our study.

The lack of independence, both within and among predictors, complicates the interpretation of our habitat models. Since our sampling unit is a grid cell, spatial autocorrelation will exist for all the independent variables that we considered (i.e., the value at a particular grid cell will not be independent of the values of its neighbours). While methods exist to extract the spatial scales of these autocorrelations (e.g., variograms), it is not clear how identifying the spatial scales of these autocorrelations would help to identify the processes and relationships of interest. Similarly, while slope and depth may be correlated to some degree, quantifying this relationship using some form of categorical analysis (i.e., principal components analysis) does not provide any additional insight into what defines whale habitat and may, in fact, complicate the analysis by introducing abstract component terms.

We accept that there is a significant lack of independence in both the dependent and the predictor data sets, and we have not attempted to correct for these effects. Consequently, the degrees of freedom reported for the results are artificially high. To some extent, this lack of independence is offset by the large sample size and the use of generalized linear models and is more a cause for debating the relative strength and scale of the proposed processes rather than a reason for dismissing the hypotheses out of hand.

Effort assumption

The assumption of equal whaling effort throughout the 150-nmi search area warrants detailed consideration, as it is central to the analysis. Based on information available on the British Columbia coastal whaling industry, whalers traveled up to 200 nmi from shore and remained at sea for several days (Pike and MacAskie 1969; Webb 1988). Captured whales were marked and floated for later recovery while the vessels pursued additional animals. Evidence for the annual movement of whaling effort further and further offshore was provided by Gregr et al. (2000) who showed that the annual mean distance from shore for animals killed changed significantly between 1948 and 1967. Thus, the whalers clearly had to move through areas that were closer to Coal Harbour with greater frequency than through areas further away. It is therefore unlikely that equal effort was expended on all 1507 grid cells within the 150-nmi area. If the monthly time scale is included, the likelihood of equal effort over all 9029 monthly grid cells becomes very small indeed. Given that the change in effort with distance could be estimated, as could the relative monthly effort, it is theoretically possible to develop a technique for weighting the contribution of individual cells based on time and space. However, this additional research and analysis was beyond the scope of our study.

Fortunately, the behaviour of the whalers likely mitigated the effect of unequal effort in both time and space. Given the practices described above, it is likely that animals of any species encountered in nearshore areas were killed prior to the whalers proceeding further offshore. This effectively eliminated any significant monthly bias towards particular species, leaving legal lengths as the only remaining bias

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(Gregr et al. 2000). Spatially, it can be assumed that the whalers operated with a fairly detailed knowledge of where whales were commonly found. The whaling captains operating from Coal Harbour had years of experience to draw upon. They were also provided with incentives to whale cooperatively and in later years relied on aerial reconnaissance (Webb 1988). Thus, it is likely that regions with few kills did in fact contain very few whales, even though they may not have been heavily searched.

Any effects of nonrandom sampling on our results would bias the predictions towards certain values of the predictor variables or cause the contributions of the individual predictors to the overall model fit to be incorrectly calculated. This is most apparent at the monthly time scale, where it can safely be assumed that equal effort was not expended in all months. While this monthly effort bias would be a serious concern if our study addressed animal abundance, limiting our interest to animal occurrence reduces its effects. Given the nature of the data, it is unlikely that this bias could be disentangled from the real process of whale migration.

Nonrandom spatial sampling (i.e., the preferential searching by whalers of some areas over others) would bias our habitat predictions towards the oceanographic conditions found in the more commonly searched areas. Since cells closer to Coal Harbour were searched with greater effort than those at a distance, by treating all cells equally, our predictions are biased to some degree towards oceanographic conditions at the more distant cells.

TIN interpolation

TINs are a standard method of representing point data. They are built by connecting data points into a series of triangles based on Delauney triangulation (Burrough and McDonnell 1998). The triangles are then used to interpolate missing values. The greater the density of point data, the smaller the triangles that are created. The accuracy of the interpolation increases with the density of the point data. Interpolations done across larger geographic areas (where point data are sparse) may fail to capture smaller scale regions of variation.

In our study, additional biases were likely introduced by edge effects and extrapolation. The outermost triangles of the TIN surface were artifacts of masking, which set the region outside the study area to zero. This made the interpolated predictor values inaccurate at the edges. In addition, a number of areas in the study area (British Columbia coast) required the predictors to be extrapolated outside the range used to define the models (i.e., within the 150-nmi radius). These extrapolations represent another type of edge effect: at the boundaries of the sampled data.

Concurrency of biological and oceanographic data

The whaling data (1948–1967) did not overlap temporally with the independent oceanographic data (pooled over the years 1980–1998). Although it is clearly more desirable to have dependent and independent measurements made concurrently, the spatial coverage of the oceanographic point data for years prior to 1967 is very poor. We therefore chose data density over data currency.

We have shown that this lack of temporal currency between the dependent and independent variables has statistically significant effects on the habitat predictions using a 10-km grid size. However, at larger spatial scales, we would expect this significance to decrease as localized differences in temperature are pooled and averaged. A more sophisticated oceanographic model is needed to explore how scale mediates the effects of changes in ocean temperature and salinity.

Despite the foregoing, areas of predicted high probability likely represent some aspect of whale habitat. The potential problems associated with the biases discussed only raise the question of the relative importance of the habitats described and do not invalidate our findings. While we may debate whether the habitats described here are "critical" or "important" or simply "suitable," the areas identified should be acknowledged as having some level of importance to these species.

Future work

Our habitat predictions could be refined through field studies and through a multiscale analysis of the predictor effects at other combinations of spatial and temporal scales. Field tests of the habitat predictions would provide some essential validation of the predictions, while tracking and long-term monitoring of these relatively depleted populations would provide contemporaneous sighting and predictor data. Conducting multiscale analyses would provide valuable information on the scale and relative strength of the predictors, leading to a better understanding of the scales over which the proposed processes operate. Other predictors (i.e., primary production, depth of mixed layer, distance to frontal features, etc.) should also be considered if they can be consistently collected concurrently with the sighting data. The fit of the model could also be improved by addressing the problems of searching effort and autocorrelation. Cells in the study grid could be weighted based on assumptions about the distribution of effort, while an analysis of the correlations within and between the variables would improve the independence of the grid cells. Applying the approach to a larger geographic area, either by adding oceanographic data from California, Washington, Oregon, and Alaska or by constructing new models using positional data from other whale fisheries in the North Pacific (i.e., the pelagic fishery), would provide valuable comparisons of scale and process.

Our work extends previous studies that have been limited to correlation analysis between whale species and various oceanographic features. We treated a suite of independent oceanographic measures as predictor variables in a generalized linear model and compared the relationships at mean annual and monthly time scales. Our study shows that, even in the presence of nontrivial spatial and temporal autocorrelation, unequal sampling effort, and a lack of concurrency between the independent and dependent variables, reasonable hypotheses can be generated using this type of retrospective analysis. Our methods provide a novel approach for generating habitat predictions based on measurements of the physical environment. The software that we developed facilitates the integration of diverse spatial data sets and provides a powerful framework for exploring and presenting the predictions of critical habitat. The ability to quickly generate and view predictions at various spatial and temporal scales is useful to the investigation of scale effects

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and the linkages between pattern and process. Our study can therefore be considered as both a preliminary set of habitat predictions for five whale species that frequent British Columbian waters and a method for constructing and exploring habitat models.

Acknowledgments

The historic whaling database was compiled by Linda Nichol and colleagues and provided by the Department of Fisheries and Oceans. We would like to thank Dr. Ian Perry and Graeme Ellis of the Pacific Biological Station and Drs. John Dower, Tony Sinclair, and Daniel Pauly of the University of British Columbia for their contribution to the interpretations of the habitat models. Suggestions by Ryan Woods and colleagues at University of British Columbia's SCARL significantly improved the model building methods and the resulting habitat predictions. Invaluable assistance in the development of the spatial analysis tools was provided by David Hawkins of Facet Decision Systems, Inc. This study was supported by an industrial Natural Sciences and Engineering Research Council of Canada scholarship to E. Gregr and a grant from the Department of Fisheries and Oceans. The software for data integration and spatial analysis and the associated computer time were kindly provided by Facet Decision Systems, Inc. Comments from two anonymous reviewers greatly improved the clarity of this manuscript.

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Appendix. Regression coefficients

Coefficients are shown for the annual and monthly models. The coefficients are for Poisson regressions. To convert to probabilities, the result is transformed according to

$$\text{(A1)} \quad \Pr(\text{Wh}) = 1 - e^{-u}$$

where u is the Poisson prediction.

The categorical variables slope, depth class, and month have a coefficient for each level, with the value for the first level = 0 (not tabulated). The coefficients for the continuous predictors are multiplied by the predictor value. Where interactions between the categorical and continuous predictors occur, there is a continuous coefficient for each level of the categorical predictor.

Table A1. Annual regression model coefficients for whale species.

	SW	FW	HW	BW	SPW-M	SPW-F
intercept	–1.98	–1660	–1.59	–2340	–2430	–8.03
slope1	–0.35	–0.308	–0.00195		–0.114	–0.297
slope2	–0.934	–0.407	0.488		–0.077	–0.138
slope3	–1.59	–0.741	0.347		–0.16	–0.61
slope4	–1.12	–0.398	0.773		0.768	–0.388
slope5	–0.931	–0.7	0.804		0.372	–1.15
slope6	–0.851	–0.371	0.679		0.817	–0.584
dclass2	1.91	0.336	0.073	2.78	2.1	
dclass3	2.64	1.15	1.22	3.52	2.84	
depth	–0.00561	–0.00498	–0.00279	–0.00382	–0.00208	–0.0074
temp	–0.516				0.459	
$temp^2$	0.0226				–0.022	
salt		105		149	154	
$salt^2$		–1.67		–2.36	–2.43	

Note: SW, sei whale; FW, fin whale; HW, humpback whale; BW, blue whale; SPW-M, male sperm whale; SPW-F, female sperm whale.

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Table A2. Monthly regression model coefficients for whale species.

	SW[a]	FW	HW[b]	SPW-M[a,b]	SPW-F
intercept	–505	–877	–1310	–28.9	–21.2
month5	8.36	0.548	2.1	–5.28	0.558
month6	7.82	1.23	3.55	–5.42	–0.991
month7	6.11	1.6	4.12	–0.532	–2.71
month8	–4.18	1.85	4.18	–1.09	–2.12
month9	3.63	1.17	3.38	–1.64	–3.81
slope1	–0.296	–0.294	–0.191	–0.19	–0.313
slope2	–0.879	–0.38	0.355	–0.171	–0.142
slope3	–1.54	–0.717	0.311	–0.222	–0.632
slope4	–1.07	–0.327	0.758	0.76	–0.41
slope5	–0.809	–0.651	0.689	0.293	–1.15
slope6	–0.809	–0.355	0.479	0.741	–0.554
dclass2	1.99	0.398	–104	40.5	–0.0072
dclass3	2.66	1.15	–785	70.6	0
depth	–0.00535	–0.00506	–0.00231	–0.00243	
salt	31.8	55.8	80.7	1.01	0.385
			89	–0.198	
			134	–1.12	
salt^2	–0.514	–0.89	–1.25		
			–1.41		
			–2.13		
temp	0.717	–0.172	–0.299	–0.924	
	–0.0662			–0.239	
	0.0425			–0.206	
	0.194			–0.525	
	0.77			–0.44	
	0.198			–0.417	

Note: SW, sei whale; FW, fin whale; HW, humpback whale; SPW-M, male sperm whale; SPW-F, female sperm whale.

[a]Interaction between temperature and month.

[b]Interaction between salinity and depth class.

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Landscape variables influencing nutrients and phytoplankton communities in Boreal Plain lakes of northern Alberta: a comparison of wetland- and upland-dominated catchments

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Abstract: A review of headwater lakes in undisturbed watersheds on the Boreal Plain, with indirect gradient analyses of chemical data, indicated a clear separation between those in wetland-dominated watersheds (57–100% wetland with variable proportions of bog, fen, swamp, and marsh cover) and those in upland-dominated watersheds (0–44% wetland cover). In the former, percentage wetland cover in the watershed was positively correlated with total phosphorus (TP, $r^2 = 0.78$, primarily bog), total nitrogen (TN, $r^2 = 0.50$), and dissolved organic carbon (DOC, $r^2 = 0.74$) concentrations. Rich fens appeared to sequester both TP and TN. In upland-dominated lakes, the ratio of catchment area to lake volume (CA/LV) was the strongest watershed correlate of TP concentration ($r^2 = 0.56$), whereas most limnetic nitrogen and DOC were generated in situ. Colour concentration, being highest in wetland lakes, was correlated with the ratio of isotopically defined effective drainage basin area to lake volume (eDBA/LV, $r^2 = 0.63$). Drainage basin slope was only weakly associated with water quality, likely because of low topographic relief (≤11%). Higher Chlorophyta and Peridineae biomasses in wetland-dominated systems than in upland-dominated ones may coincide with greater NH_4^+ availability.

Résumé : Une analyse indirecte de gradient des données chimiques provenant de lacs situés en amont de bassins hydrographiques non perturbés de la Plaine boréale indique une nette séparation entre les lacs provenant de bassins dominés par les terres humides (57–100% de terres humides, avec des proportions variables de couverture de tourbières ombrotrophes, de tourbières minéralotrophes, de marécages et de marais) et ceux des bassins dominés par des terres hautes (0–44% de terres humides). Chez les premiers, le pourcentage de couverture par les terres humides dans le bassin est en corrélation positive avec les concentrations de phosphore total (TP, $r^2 = 0{,}78$, surtout des tourbières ombrotrophes), d'azote total (TN, $r^2 = 0{,}50$) et de carbone organique dissous (DOC, $r^2 = 0{,}74$). Les tourbières minéralotrophes productives semblent accaparer le TP et le TN. Dans les lacs provenant de bassins dominés par les terres hautes, le rapport de la surface du bassin hydrographique sur le volume du lac (CA/LV) est la variable qui montre la plus forte corrélation avec la concentration de TP ($r^2 = 0{,}56$); la majorité de l'azote et du DOC limnétiques y sont générés in situ. La couleur, qui est à son maximum dans les lacs des bassins dominés par les terres humides, est en corrélation avec le rapport de la surface effective du bassin de drainage (mesurée à l'aide d'isotopes) et le volume du lac (eDBA/LV, $r^2 = 0{,}63$). La pente du bassin versant n'est que peu associée à la qualité de l'eau, probablement parce que le relief topographique est faible (≤11%). Les biomasses plus élevées des chrorophytes et des péridiniens dans les lacs dont le bassin est dominé par les terres humides sont sans doute associées à une disponibilité plus grande du NH_4^+.

[Traduit par la Rédaction]

Received November 28, 2000. Accepted March 28, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 4, 2001.
J16113

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 DOI: 10.1139/cjfas-58-7-1286 © 2001 NRC Canada

Introduction

The Boreal Forest covers over one-fifth of Canada's landmass. Geological and climatic variation across this land base result in two major subregions: the larger, wetter, and nutrient-poor Boreal Shield of central and eastern Canada and the drier, nutrient-rich Boreal Plain of western Canada. On the Boreal Shield, differences in lake morphometry, drainage basin topography, and land use explain variability in water quality (Schindler 1971; Dillon et al. 1991; D'Arcy and Carignan 1997); similar relationships have yet to be developed for the Boreal Plain. Lakes on the Boreal Plain are situated on low-relief, often poorly drained sedimentary tills in contrast to the typically higher relief of Shield drainages (Mitchell and Prepas 1990). Relative to lakes on the Boreal Shield, lakes on the Boreal Plain tend to be phosphorus- (P) and plankton-rich (D'Arcy and Carignan 1997; Mitchell and Prepas 1990). On an annual basis, euphotic total phosphorus (TP) in lake water on the Boreal Plain is derived mainly through internal sediment P recycling (Shaw and Prepas 1990), atmospheric P inputs being relatively unimportant compared with Boreal Shield lakes (Shaw et al. 1989; D'Arcy and Carignan 1997). In summer, high cyanobacterial biomass is typical of phytoplankton communities on the Boreal Plain (Zhang and Prepas 1996), whereas Chrysophytes and other flagellates dominate Boreal Shield communities (Planas et al. 2000). Given differences in drainage basin geomorphology, nutrient dynamics, and phytoplankton communities, in situ models developed for drainage basin water quality interactions on the Boreal Shield (e.g., Rasmussen et al. 1989) for colour and dissolved organic carbon (DOC) will likely require modifications for the Boreal Plain.

Another feature distinguishing the two Boreal subregions is the amount and type of wetlands, the Boreal Plain (Alberta) having more than twice the wetland (bogs, fens, marshes, and swamps) coverage of the Boreal Shield (Québec) (NWWG 1998). The extent of peatland (i.e., bogs and fens) coincides with increased dissolved nitrogen, phosphorus, and organic carbon concentrations in lakes on the Boreal Plain (Halsey et al. 1997) and Boreal Shield (Dillon et al. 1991). Peatlands can vary markedly in water discharge and thus in their influence on surface water chemistry (Halsey et al. 1997). The amount of water produced by surface and subsurface flow forms an effective watershed (effective drainage basin area, eDBA, defined with stable isotopes by Gibson and Prowse 1998) within the total drainage basin. The size of an eDBA depends on the resistance that water encounters flowing from precipitation to lake and on surface storage, soil storage, hydraulic conductivity, groundwater levels, and the seasonal water balance (Soranno et al. 1996). Effective drainage basin area may be more closely linked with water quality in regions such as the Boreal Plain, where low drainage basin slope and variable runoff are associated with extensive peatland cover.

Data collected from headwater lakes having watersheds with minimal disturbance and near zero to 100% wetland cover in their watersheds were used to test hypotheses generated from studies based primarily on the Precambrian Shield and for peatland-dominated lake basins. These hypotheses are as follows: (*i*) physical features, such as water residence time, lake depth, drainage basin area (DBA) to lake area (LA) ratio (DBA/LA, where DBA = catchment area (CA) – LA), slope, and vegetation cover are effective predictors of lakewater TP concentrations; (*ii*) nitrogen concentrations will be higher in wetland-dominated systems; (*iii*) phytoplankton communities within wetland-dominated systems will have higher biomasses of N-dependent (non-nitrogen-fixing) taxa than upland-dominated systems; (*iv*) in-lake DOC and colour are related to the extent of wetland coverage within drainage basins; and (*v*) eDBA is a better predictor of constituent inputs than DBA or CA, particularly in wetland-dominated watersheds.

Materials and methods

Study area

Euphotic water quality and phytoplankton samples and morphometric and watershed characteristics were collected for 26 headwater lakes located within a 109 600-km^2 area (Fig. 1) within the mixed-wood ecoregion of the Boreal Plain ecozone (Strong 1992). Soil types within the study region range from eutric brunisols–gray luvisols in upland areas to organics–gleysols in wetland areas. Boreal Plain wetlands are categorized as peatland (bogs, poor fens (PFEN), and rich fens (RFEN)) and non-peatland (swamps and marshes (SWAMP)) (Halsey et al. 1997). Bogs are dominated by Bryophytes, notably *Sphagnum*, and tree cover, when present, is limited to *Picea mariana*. Fens vary in cover from open (dominated by *Carex*, *Scirpus*, and *Eriophorum*), shrubby (*Betula* and *Salix*), to wooded (*Picea mariana*, *Larix laricina*, *Betula*, and *Salix*). Swamps and marshes are predominately forest–shrub (swamps) and *Carex–Scirpus–Typha* (marshes). Boreal mixed-wood uplands are dominated by *Populus tremuloides*, *Populus balsamifera* (DECID), and *Picea glauca* (CONIF) stands, with a diverse understorey of herbs and shrubs (Strong 1992). Thirty-year average annual precipitation for the region ranged from 388 to 432 mm (33% as snow), and mean annual air temperature ranged from 0.7 to 1.4°C. During the main sampling periods (June–September 1996 and 1997), the region received twice the average precipitation compared with the 30-year normal, depending on location (Environment Canada, Commercial Weather Service, Edmonton, Alta., unpublished data). The two main sampling years were relatively wet. The lakes chosen were either slated for or near those slated for harvesting in or around 1997 or near areas burned in the 1995 wetland-dominated fires. None of the study systems has been disturbed (>5% of vegetation removed) within the past 50 years.

Sampling and analyses

Eleven lakes were sampled monthly by fixed-wing aircraft with pontoons during early to mid-July, August, and September 1996 and 1997. Another 11 lakes (N11, N31, N32, N33, N34, N35, N37, N38, N39, N40, and N41) were ground-accessible. Nine of these lakes were sampled at 2- to 3-week intervals and two lakes were sampled at 1- to 2-week intervals from mid-June to mid-August 1996. As the watersheds of 10 of the 11 ground-accessible lakes were harvested in winter of 1997, 1997 data from only one of these could be included in our analyses. Long, Moore, Narrow, and Sauer lakes (Fig. 1) were sampled on one date between mid-August to early September 1998. To summarize, 12 lakes had water quality data available for 1996 and 1997, 10 lakes had data available for 1996, and 4 lakes had data for 1998 only, for a total of 38 independent summer observations of water quality on 26 lakes. Each of these 38 independent estimates represents summer mean euphotic water quality based on one (n = 4), three (n = 22), four to five (n = 10), or nine to ten (n = 2) sampling dates.

Vertically integrated water samples were collected from the euphotic zone (depths receiving ≥1% of ambient surface light) at two sites (including the deepest) along the longitudinal axis of each lake. Light extinction coefficient (ϵ) was calculated from pro-

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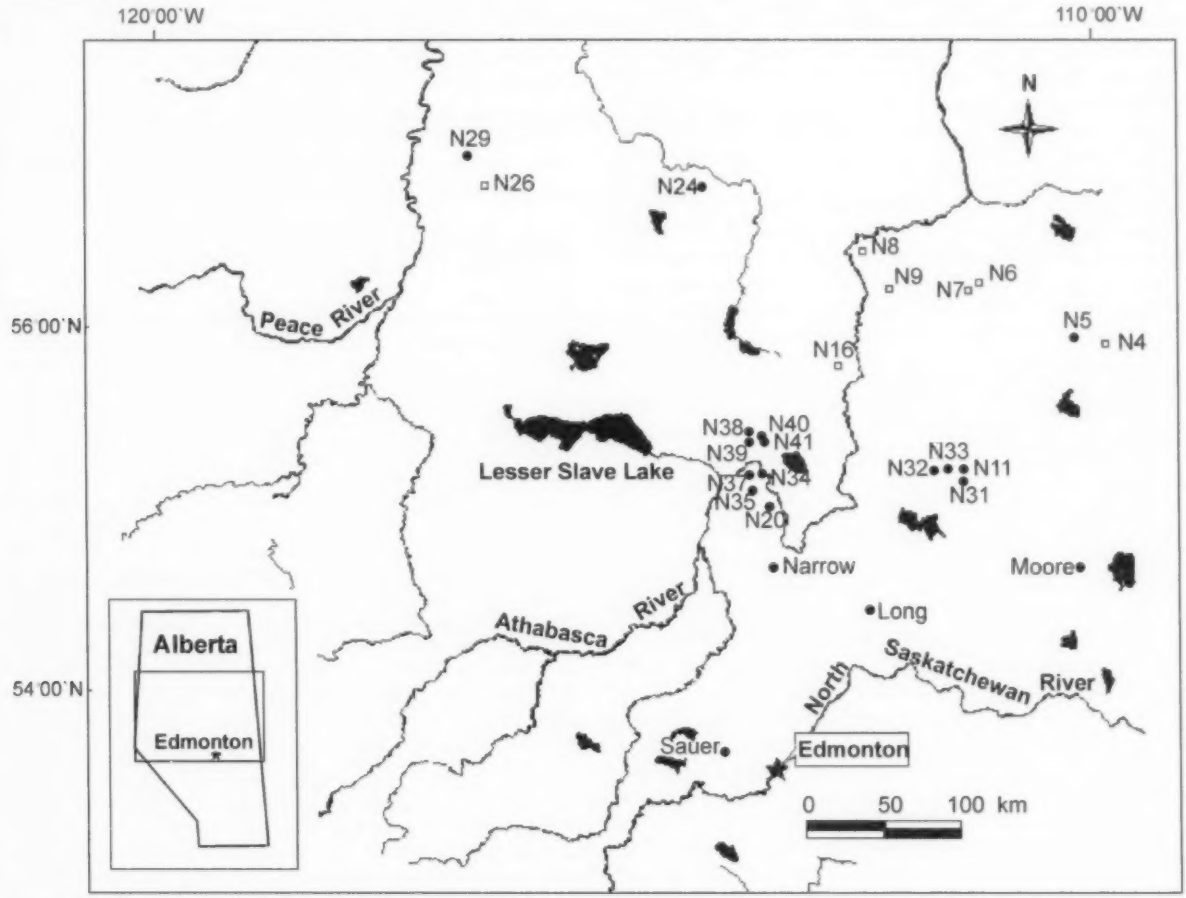
Fig. 1. Location of the Boreal Plain study lakes. Open squares denote wetland-dominated systems; solid circles denote upland-dominated systems.



file data measured at the deepest site with a LiC or LI-1000 meter; data were unavailable for Long, Moore, Narrow, and Sauer lakes. Samples for chlorophyll *a* (Chl *a*) analysis were filtered through Whatman GF/C filters at –50 kPa and frozen within 12 h of collection. Filtrate from distilled–deionized water-rinsed, 0.45-μm Millipore HAWP membranes was used for total dissolved phosphorus (TDP) and nitrate + nitrite ($NO_3 + NO_2$) analyses. Samples for TP, TDP, pH, colour, alkalinity, and conductivity were analysed within 24 h. $NO_3 + NO_2$ and ammonium (NH_4) samples were preserved with H_2SO_4 and then refrigerated for 1–2 weeks before analysis. Total dissolved nitrogen (TDN) samples were filtered through preweighed, Whatman GF/C filters, refrigerated, and analysed within 48 h. Filters were then vacuum-desiccated and frozen for subsequent particulate N (PN) analysis. Samples for major cations (Ca, Mg, Na, K), major anions (Cl, SO_4), and DOC were filtered through precombusted Whatman GF/C filters before long-term (1–2 months) storage. Samples for major cations and DOC analyses were acidified to pH < 2 with HNO_3 and then refrigerated. Samples for major anions were refrigerated only. Refrigeration was at 4°C.

Chl *a* was analysed by Ostrofsky's spectrophotometric-based ethanol extraction technique which does not correct for phaeo pigments (Bergmann and Peters 1980). TP and TDP were analysed by a modified potassium persulfate method (Prepas and Rigler 1982). pH was measured in the laboratory with a Fisher Scientific Accumet 925 pH meter. Colour (Col) was measured at 440 nm with a Milton Roy 1001 spectrophotometer (Cuthbert and del Giorgio 1992) and reported as $mg \cdot L^{-1}$ platinum (Pt). Conductivity was measured with a Radiometer CDM 83 meter. Alkalinity (primarily HCO_3) was determined on a Mettler DL 21 autotitrator. TDN samples were photocombusted in an ultraviolet digester and analysed. $NO_3 + NO_2$ and NH_4 were analysed with a Technicon autoanalyser (Stainton et al. 1977). PN was combusted at 700°C and analysed on a Control Equipment Corporation 440 Elemental Analyzer. Dissolved inorganic nitrogen (DIN) is the sum of $NH_4 + NO_3 + NO_2$, and total nitrogen (TN) is the sum of TDN + PN. Sulphate (SO_4) and chloride (Cl) analyses were run on a Dionex 2000i/SP ion chromatograph fitted with an AS4A-Sc high-capacity anion exchange column, and major cations were analysed on a Perkin Elmer 3300 atomic absorption spectrophotometer. Silica (Si) concentrations were determined spectrophotometrically (Environment Canada 1979). For DOC, sparged subsamples were run on an Ionics Corporation 1505 programmable carbon analyser with a platinum catalyst. Where direct measurements were unavailable for conductivity (COND) (14 lakes during 1996), it was estimated from the sum of mean July to September Na, K, Ca, and Mg concentrations ($mg \cdot L^{-1}$), weighted by atomic weight, based on an empirical model ($r^2 = 0.91$, df = 63) developed with data from this study ($n = 24$) and unpublished data (E. Prepas; $n = 39$):

$$(1) \quad COND = 13.77 + 102.43 \sum cations$$

Phytoplankton were identified for the 22 Boreal Plain lakes sur-

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veyed during 1996 and 1997; data were unavailable for Long, Moore, Narrow, and Sauer lakes. Duplicate phytoplankton samples were collected concomitantly with water quality, preserved on-site with Lugol's solution, and stored in amber glass bottles. Phytoplankton cells were identified, measured, and counted with a Leica DM-IRB inverted microscope (for 40× magnification, 15 to 30 fields; for 10×, ½ the slide). Cyanobacteria, Cryptophyceae, Bacillariophyta (diatoms), Euglenophyceae, Peridineae, Chlorophyta, and Chrysophyceae were identified. Cyanobacteria were subdivided into major taxa (Oscillatoriales, Nostocales, *Microcystis* spp., and other Chroococcales) and functional groups (N_2-fixing taxa, Nostocales; non-N_2-fixing taxa, Chroococcales and Oscillatoriales). Total and taxa biomasses were estimated from cell biovolume measurements (Lewis 1976), using equivalent geometric forms and assuming 1 μm^3 = 1 pg.

Lake morphometric variables (surface area (LA), volume (LV), and mean (Z_{mean}) and maximum (Z_{max}) depths) were estimated from bathymetric maps. Depths recorded along several transects per lake were digitized as binary point vector files with the software program DigiEdit. Bathymetric contour lines were created with the statistical package SYSTAT, Version 6.0. Drainage basin area and percentage coverage by bogs, fens (rich and poor), swamps, marshes, upland deciduous and coniferous stands, and open water were estimated from 1 : 20 000 or 1 : 15 000 aerial photographs. Drainage basin (DBA), lake surface area, and their sum, catchment area (DBA + LA = CA), lake volume, and mean and maximum depths for Long, Moore, Narrow, and Sauer lakes are from Mitchell and Prepas (1990). Mean drainage basin slopes (Table 1) were estimated for each drainage from 10 to 18 transects plotted regularly to reflect the size of the drainage basin, from outer boundary to shoreline on 1 : 50 000 topographic maps.

Water residence times (τ, years) were calculated for the 22 lakes sampled during 1996 and 1997 with a steady-state isotope mass-balance model, based on observed evaporative enrichment of lake water oxygen ($^{18}O/^{16}O$) and hydrogen ($^2H/^1H$) stable isotope ratios (Gibson et al. 1993). The isotope mass-balance reflects the major components of a water balance such that inflow (I), total outflow (Q), and total lake evaporation (E), in $m^3 \cdot year^{-1}$, were multiplied by the respective isotope composition ($\delta^{18}O$ and δ^2OH, ‰ Standard Mean Ocean Water (SMOW)) independently substituted for δ values to permit a comparative assessment of model uncertainty:

$$(2) \qquad I \cdot \delta_I = Q \cdot \delta_Q + E \cdot \delta_E$$

where it was assumed that the isotope composition of outflow was equivalent to the composition of lake water (δ_L), the composition of inflows was equivalent to precipitation (δ_P), and the composition of evaporated moisture (δ_E) was predicted from a model for free-surface evaporation (Gibson et al. 1993). When rearranged eq. 2 becomes

$$(2a) \qquad E/I = (\delta_L - \delta_P) \cdot [m(\delta^* - \delta_L)]^{-1}$$

where $m = h(1 - h)^{-1}$ and h is ambient atmospheric humidity. Limiting isotopic enrichment (δ^*) was equivalent to $\delta_h + \varepsilon \cdot h^{-1}$, where δ_h is the isotopic composition of atmospheric humidity and ε is the isotopic fractionation factor, which is dependent on mean annual air temperature (Gibson et al. 1993). Mean annual isotopic composition (δ_L) was determined from lake water collected in July, August, and September of 1996 and 1997. Other parameters required to calculate E/I (δ_P, δ_h, h, and mean annual air temperature) were interpolated for each lake from Environment Canada climate station data and the Global Network for Isotopes in Precipitation database (IAEA/WMO 1999). Specific assumptions on the boundary layer regime and atmospheric parameters used in the model are discussed in Gibson and Prowse (1998). Once the relative fraction of evaporation to inflow was calculated, lake water residence time was

$$(2b) \qquad \tau = ((E/I) \cdot Z_{mean}) \cdot E_L^{-1}$$

where Z_{mean} is mean lake depth (m) and E_L^{-1} is long-term mean annual lake evaporation rate ($mm \cdot year^{-1}$) for the region (Environment Canada 1978). Water residence times for Long, Moore, Narrow, and Sauer lakes are based on 25-year averages of precipitation, runoff, and evaporation (Mitchell and Prepas 1990). Effective DBA (eDBA, km^2) was calculated as

$$(3) \qquad \text{eDBA} = (R \cdot P^{-1}) \cdot \text{DBA}$$

where R and P are mean annual drainage basin runoff and precipitation (both in $mm \cdot year^{-1}$), respectively.

To put the lakes surveyed in 1996 and 1997 in a context with others studied on the Boreal Plain, comparable summary information was prepared for lakes in the Atlas of Alberta Lakes (Mitchell and Prepas 1990); the latter analyses excluded the four headwater lakes added to our data analyses from the Atlas (Table 1). The data set for comparison consisted of 42 small to moderate-sized lakes north of the City of Edmonton.

To test hypotheses on the relationship between drainage basin vegetation and physiography and water quality, an indirect gradient analysis with a linear model was performed in CANOCO Version 4.0 (ter Braak and Smilauer 1998). Because of collinearity between environmental variables, only the following were included in the final analyses: LV, LA, τ, Z_{mean}, Z_{max}, DBA/LA, DBA/LV ($km^2 \cdot 10^5$ m^{-5}), CA/LV, % CONIF, % PFEN, % peatland (bog + fen), % bog, % upland, % DECID, slope, and elevation. Percentage vegetative cover is relative to drainage basin area throughout. A "passive analysis" of environmental variables and unconstrained ordination axes by correlation determined the relationship between lake chemistry and the corresponding DB vegetation and physiography.

Relationships between water quality and drainage basin – morphometric variables were examined by least squares methods of multivariate linear regression. Variable data with non-normal distributions (Shapiro–Wilks' test) were $\log_{10}$- or arcsine-transformed, where appropriate. Pearson's correlation matrices were generated to select independent variables for regression analyses, based on significant ($P \leq 0.01$) correlations with dependent (water quality) variables and to detect intercorrelation between independent variables. Only the strongest, in terms of percentage variation ($r^2 \times 100$) explained, and the most limnologically meaningful relationships are presented (*, $P < 0.05$; **, $P < 0.01$). Student's t tests were performed for data with heterogeneous variances, where appropriate. All analyses were performed with SPSS for Windows version 8.0.

Results and discussion

The lakes surveyed during 1996 and 1997 (Table 1) are smaller and shallower (mean LA and Z_{mean} = 0.8 km^2 and 2.3 m, respectively, n = 22) than Boreal Plain lakes from the Atlas of Alberta Lakes (Mitchell and Prepas 1990) (mean LA and Z_{mean} = 31 km^2, n = 42, and 6.7 m, n = 41, respectively; Table 2). Consequently, four small headwater lakes in undisturbed watersheds, Long, Moore, Narrow, and Sauer (mean LA and Z_{mean} = 4.1 km^2 and 7.8 m, respectively, n = 4) were added to our survey set to better reflect the range of physical characteristics reported for the Boreal Plain (Table 2). Mean DBA/LV of these four systems was one-quarter that for the other upland-dominated systems in our data set (1.3 vs. 5.2, respectively), but other physical parameters did not differ overall despite noticeable extremes in individual systems (Table 1). Water quality in Long, Moore, Narrow, and Sauer lakes, with the exception of colour (13 $mg \cdot L^{-1}$ and 43 $mg \cdot L^{-1}$ Pt, respectively), did not differ detectably

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Table 1. Drainage basin and lake morphometry data for the 26 study lakes.

Lake	Catchment type	Year(s) surveyed	DBA (km^2)	LA (km^2)	LV ($m^3 \times 10^6$)	DBA/LV	CA/LV	Z_{mean} (m)	Z_{max} (m)	SLOPE (%)	CONIF (%)	DECID (%)	WETL (%)
N4	Wetland	1996, 1997	0.56	0.19	0.19	2.9	3.9	1.0	5.5	3.9	43	0	57
N6	Wetland	1996, 1997	4.28	0.90	0.96	4.5	5.4	1.1	1.8	0.8	28	0	71
N7	Wetland	1996, 1997	1.87	1.01	1.47	1.3	2.0	1.5	3.3	0.8	43	0	57
N8	Wetland	1996, 1997	9.14	0.69	0.46	19.9	21.1	0.7	1.8	0.5	8	0	92
N9	Wetland	1996, 1997	18.80	1.62	1.73	10.9	11.8	1.1	1.8	0.3	5	2	93
N16	Wetland	1996, 1997	6.99	1.62	2.08	3.4	4.1	1.3	1.8	0.6	0	0	100
N26	Wetland	1996, 1997	16.22	2.00	5.72	2.8	3.2	2.9	5.8	1.0	20	20	60
N5	Upland	1996, 1997	5.15	1.20	1.38	3.7	4.6	1.2	4.6	1.4	29	28	44
N11	Upland	1996	6.12	0.62	2.40	2.6	2.8	3.9	5.8	8.0	7	83	10
N20	Upland	1996, 1997	4.52	0.30	0.27	16.7	17.8	0.9	1.8	3.3	26	61	11
N24	Upland	1996, 1997	1.51	0.25	0.49	3.1	3.6	1.9	4.0	6.6	14	65	20
N29	Upland	1996, 1997	2.58	1.70	2.32	1.1	1.8	1.4	2.4	2.6	24	33	24
N31	Upland	1996	1.09	0.14	0.37	2.9	3.3	2.7	5.5	4.7	9	85	5
N32	Upland	1996	1.89	0.33	0.56	3.4	4.0	1.7	4.1	3.3	4	73	22
N33	Upland	1996	4.55	1.04	3.30	1.4	1.7	3.2	7.2	3.6	3	83	14
N34	Upland	1996	6.78	0.52	2.53	2.7	2.9	4.9	11.2	3.5	6	81	11
N35	Upland	1996	2.92	0.18	0.72	4.1	4.3	3.9	7.6	3.0	3	70	25
N37	Upland	1996, 1997	7.42	0.75	1.67	4.4	4.9	2.2	2.9	1.1	1	82	16
N38	Upland	1996	10.53	1.57	7.16	1.5	1.7	4.6	8.5	4.5	43	45	13
N39	Upland	1996	8.40	0.56	0.72	11.7	12.5	1.3	2.3	3.9	19	59	21
N40	Upland	1996	9.64	0.45	2.00	4.8	5.1	4.4	9.1	3.7	29	59	13
N41	Upland	1996	6.50	0.65	1.57	4.2	4.6	2.4	3.9	3.9	15	59	21
Narrow	Upland	1998	7.17	1.14	16.40	0.4	0.5	14.4	38.0	3.4	25	52	21
Sauer	Upland	1998	0.49	0.09	0.35	1.4	1.6	4.2	8.5	10.6	40	60	0
Long	Upland	1998	82.40	5.84	29.30	2.8	3.0	4.3	9.0	3.4	15	83	0
Moore	Upland	1998	37.10	9.28	77.40	0.5	0.6	8.3	26.0	2.6	21	48	23

Note: DBA, drainage basin area; LA, lake area; LV, lake volume; DBA/LV, drainage basin area/lake volume; CA/LV, catchment area/lake volume; Z_{mean}, mean depth; Z_{max}, maximum depth; CONIF, conifer; DECID, deciduous; WETL, wetland. DBA, LA, LV, Z_{mean}, and Z_{max} for Narrow, Sauer, Long, and Moore lakes are from Mitchell and Prepas (1990).

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from that of the other upland-dominated systems. We also looked at differences between water quality data for Long, Moore, Narrow, and Sauer lakes collected on one date in 1998 and historical data collected on the same lakes on several dates during the early 1980s (Mitchell and Prepas 1990). Differences were as high as 21% and 25% (Chl *a* and conductivity, respectively) but were <13% for TP and dominant ions and only 4% for alkalinity and pH. Although parameters such as nutrients and Chl *a* vary seasonally, deep lakes such as Long, Moore, Narrow, and Sauer are relatively stable compared with shallower lakes, and thus one sampling date can give a reasonable approximation of water quality for pattern generation (Prepas and Trimbee 1988). The inclusion of these lakes allowed us to assemble the best data set available to address our objectives.

Most previously studied Boreal Plain lakes are located in road-accessible, inhabited areas of Alberta, where wetlands were sometimes drained for agricultural or other water management purposes (Mitchell and Prepas 1990). In these lakes, alkalinity, conductivity, pH, and base cation concentrations were on average higher (Table 2) than in our study lakes with relatively unperturbed drainages (Table 3). However, our study lakes reflect the range of trophic conditions in the Boreal Plain in that ranges in TP, Chl *a*, NO_3, and DOC concentrations are comparable with data for the region (Tables 2 and 3).

Lake productivity indices were up to an order of magnitude higher compared with those of D'Arcy and Carignan's (1997) Boreal Shield lakes (mean TP, 54 $\mu g \cdot L^{-1}$ and 8.7 $\mu g \cdot L^{-1}$; Chl *a*, 19 $\mu g \cdot L^{-1}$ and 2.7 $\mu g \cdot L^{-1}$, respectively). Although mean DBA in this study is larger than that of the Shield study (10 km^2 and 2.3 km^2, respectively), drainage ratios were similar (mean DBA/LA, 8.3 and 7.5, respectively). Wetland coverage per drainage basin in this study was on average 25 times that reported for the Shield study (32% and 1.3%, respectively). Upland conifer cover in Boreal Plain systems averaged less than half that of Shield systems (18% and 44% of DBA, respectively).

Indirect gradient analysis of chemical data indicated a clear separation between lakes with >50% wetland (range 57–100%) and those with <50% wetland (range 0–44%) in their watershed. Our division between wetland and upland is arbitrary and only a much larger study would permit evaluation of whether the relationship is a continuum or discontinuous. Four of the seven wetland-dominated systems were far to the right in the ordination (N6, N8, N9, N16, >71% wetland). Two more wetland lakes (N4, N7, both 57% wetland) were also to the right of all the upland-dominated systems, along with colour and inorganic nitrogen concentrations, whereas the remaining lakes were in the centre and left-hand portion (Fig. 2). The seventh lake (N26) with >50% wetland in the drainage was the only wetland-dominated lake with a substantive amount of deciduous trees (20% compared with 2% or less; Table 1) in its catchment; the remaining wetland-dominated catchments were conifer dominated in their upland sections. N26 rested in the middle of the lakes with upland-dominated drainages. Initial review of the data gave no indication of systematic changes introduced by having more data available for the first of the two wet years (1996, 1997) of this study. The gradient analysis confirmed that vegetative features of the catchment including percentage wetland and percentage upland and physical features related to relative drainage basin area were substantive contributors to water chemistry. This initial data compilation suggested that in addition to relationships with the entire data set (ALL), we should explore independently those with wetland- and upland-dominated catchments.

When the lakes were divided into wetland- and upland-dominated systems, the physical and chemical differences suggested by gradient analyses were apparent (Tables 3 and 4). Mean and maximum depths were over 2.5-times greater as were drainage basin slopes, whereas eDBA were 2.5 times smaller in lakes with upland-dominated drainage basins; however, other morphometric and physical drainage basin parameters were not detectably different. Bogs and deciduous forest were the dominant vegetation in wetland- and upland-dominated drainages, respectively. Although mean in-lake TP, Chl *a*, and TN concentrations were similar ($P > 0.5$), wetland-dominated systems were on average more coloured with lower pH and conductivity than upland-dominated systems (186 $mg \cdot L^{-1}$ vs. 38 $mg \cdot L^{-1}$ Pt, 5.7 $\mu S \cdot cm^{-1}$ vs. 7.6 $\mu S \cdot cm^{-1}$, and 265 $\mu S \cdot cm^{-1}$ vs. 80 $\mu S \cdot cm^{-1}$, respectively, $P < 0.001$ for all comparisons).

Within the combined data set, DBA/LV was strongly linked to Chl *a*, TP, and colour ($r = 0.58$, 0.62, and 0.64, respectively, $P << 0.01$), less strongly to TDP ($r = 0.49$, $P < 0.05$), and not detectably to nitrogen. Associations between CA/LV and DBA/LV were indistinguishable. Water residence was negatively related to TP and DOC ($r = -0.45$, –0.46, respectively, $P < 0.05$) and colour ($r = -0.84$, $P << 0.01$). Presence of wetlands in the drainage, particularly bogs, were positively linked to lakewater DOC concentrations and colour ($r = 0.58$ and 0.78, respectively) and negatively associated with lakewater pH, alkalinity, base cation concentrations, and conductivity (Na, $r = -0.42$, $P < 0.05$; for the rest, –0.55 to –0.71, $P < 0.001$). Drainage basin slope was not related to nutrient concentration in this study in direct contrast to the Precambrian Shield (D'Arcy and Carignan 1997), probably because slopes were on average lower and covered a smaller range compared with the Shield study (ranges 0.3–11% and 6–31%, respectively). We removed Long, Moore, Narrow, and Sauer lakes to determine if these deep lakes had influenced any of the relationships and re-examined our correlation matrix. Relationships between Chl *a*, TP, TDP, DOC, colour, DBA/LV, and water residence time did not change appreciably with the removal of the four deeper lakes.

Phosphorus and drainage basin features

In the combined data set, TP concentrations were most strongly related to CA/LV (Fig. 3*a*); almost 60% of TP variability was explained by a combination of CA/LV and RFEN cover (eq. 4). DBA/LV explained essentially the same variability in TP as CA/LV (39% and 42%, respectively). In contrast to our initial hypotheses, TP concentrations in Boreal Plain lakes with relatively low watershed slope (≤11%) were unrelated to watershed slope.

$$(4) \quad \text{ALL: } \log(\text{TP}) = 1.57 + 0.38\log(\text{CA/LV})^{**} - 0.48\arcsin(\text{RFEN})^{**}, \; r^2 = 0.59.$$

In upland-dominated systems, CA/LV alone explained 56% of TP variability, with percentage fen cover explaining an

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Table 2. Summary data for Boreal Plain lakes from Mitchell and Prepas (1990).

	n	Mean	SE	Min.	Max.
Lake area (km^2)	42	31	9.1	0.2	288
Drainage basin area (km^2)	42	369	110	1.5	4040
Mean depth (m)	41	6.7	0.7	1.3	17
Maximum depth (m)	42	17	1.9	3.5	60
Chlorophyll *a* ($\mu g \cdot L^{-1}$)	37	22	3.5	3.3	99
TP ($\mu g \cdot L^{-1}$)	39	57	7.8	9	193
NO_3^- ($\mu g \cdot L^{-1}$)	32	11	2.4	1	79
DOC ($mg \cdot L^{-1}$)	22	17	1.7	10	37
Alkalinity ($mg \cdot L^{-1}$)	42	176	14	49	556
pH	42	8.0	—	7.3	9.2
Ca^+ ($mg \cdot L^{-1}$)	40	29	1.5	11	53
Cl^- ($mg \cdot L^{-1}$)	35	2.9	0.6	0.9	17
K^+ ($mg \cdot L^{-1}$)	40	8.5	1.0	0.8	25
Conductivity ($\mu S \cdot cm^{-1}$)	41	378	31	117	1143

Note: Narrow, Sauer, Long, and Moore lakes are excluded. SE, ± 1 standard error; Min., minimum; Max., maximum; TP, total phosphorus; DOC, dissolved organic carbon.

additional 20% (eq. 5). Schindler (1971) suggests a similar relationship between P and CA/LV for Boreal Shield lakes, considering that phytoplankton (Chl *a* concentration and midsummer phytoplankton production and biomass) are positively related to CA/LV. Relative watershed size is a strong driving factor for TP concentration in our upland lakes, producing 10 times more phosphorus per unit DBA than lakes on the Precambrian Shield (Carignan et al. 2000).

$$\text{(5)} \quad \text{UPLAND: } \log(\text{TP}) = 1.55 + 0.54\log(\text{CA/LV})^{**} - 0.67\arcsin(\text{RFEN})^{**},\ r^2 = 0.76$$

In wetland-dominated systems, percentage wetland (WETL) and conifer cover explained most of the TP variance (78% and 87%, respectively). Addition of sampling year (YEAR) for lakes in the wetland-dominated drainages added 7% to the TP variability accounted for by percentage wetland cover (eq. 6).

$$\text{(6)} \quad \text{WETLAND: } \log(\text{TP}) = -222.17 + 0.01(\text{WETL})^{**} + 0.11\text{YEAR}^{*},\ r^2 = 0.85$$

Consistent with our preliminary data review, the relationship between percentage wetland coverage and lakewater TP concentration (Fig. 3*b*) suggests that our systems are from two populations, one with a positive link overall between wetland cover and TP, the other with a TP-sequestering aspect associated with rich fens. By separating wetland cover into its three constituents, we see that bogs apparently release TP ($r = 0.84$, $P << 0.01$), poor fens play a neutral role ($P > 0.3$), and like our upland-dominated systems, rich fens sequester TP ($r = -0.77$, $P << 0.01$). As reported with bogs in the watersheds of our study lakes, Dillon et al. (1991), D'Arcy and Carignan (1997), and Halsey et al. (1997) also reported positive relationships between wetland coverage and water-column P concentration, despite the relatively low wetland coverage of the first two studies (up to 25 and 6%, respectively). Apparently, wetlands with organic soil do not retain P as effectively as forested systems (Halsey et al. 1997).

Nitrogen and drainage basin features

Consistent with our hypotheses, nitrogen concentrations were related to type and extent of wetland cover. Mean DIN for our upland-dominated lakes was comparable with values reported by D'Arcy and Carignan (1997) for Boreal Shield lakes (40 $\mu g \cdot L^{-1}$ and 31 $\mu g \cdot L^{-1}$, respectively). Yet most (~80%) DIN was NH_4 in the Boreal Plain lakes compared to NO_3 in D'Arcy and Carignan's (1997) Boreal Shield study. The predominance of NH_4 in Boreal Plain lakes was due to greater wetland cover and water-logged soils, which should favour the export of reduced nitrogen species such as NH_4 (Dillon et al. 1991). As a result, percentage wetland cover explained 40% of NH_4 variability in the wetland-dominated systems ($r^2 = 0.39$, $P < 0.01$).

The TN pool in our study lakes was composed of 75% TDN on average (Table 3), of which >90% was dissolved organic nitrogen. In the combined data set, mean and maximum depth and percentage rich fen and upland conifer coverage were inversely related to TN concentrations but explained ≤35% of the variation. However, when watersheds were separated based on >50% and <50% wetland coverage, TN was strongly related with percentage upland conifer ($r = -0.88$, $P < 0.001$), wetland ($r = 0.71$, $P < 0.01$), bog ($r = 0.64$, $P < 0.05$), rich fen cover ($r = -0.61$, $P < 0.05$), and eDBA ($r = 0.69$, $P < 0.01$) in the former, whereas TN was negatively linked to Z_{max} in the latter ($r = -0.74$, $P < 0.001$). Mean lake depth and wetland parameters together accounted for >70% of TN concentration variation (eqs. 7 and 8):

$$\text{(7)} \quad \text{WETLAND: } \log(\text{TN}) = 1.99 + 0.89\arcsin(\text{WETL})^{**} + 0.80\log(Z_{\text{mean}})^{**},\ r^2 = 0.91$$

$$\text{(8)} \quad \text{UPLAND: } \log(\text{TN}) = 3.39 - 0.56\log(Z_{\text{mean}})^{**} - 0.52\arcsin(\text{RFEN})^{**},\ r^2 = 0.72$$

Wetlands immediately adjacent to our upland-dominated lakes are fens, which appear to retain nitrogen to some degree (Halsey et al. 1997), whereas bogs that form the majority of total wetland area export nitrogen, similar to the bogs elsewhere in Alberta (Halsey et al. 1997) and on the Shield

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Table 3. Summary water quality data for the 26 Boreal Plain study lakes.

		Wetland-dominated (n = 14)				Upland-dominated (n = 24)					Total (n = 38)	
Variable	Abbreviation	Mean	SE	Min.	Max.	Mean	SE	Min.	Max.	P	Mean	SE
TP ($\mu g \cdot L^{-1}$)	TP	57	9.4	26	162	52	6.8	12	160	0.67	54	5.5
TDP ($\mu g \cdot L^{-1}$)	TDP	19	2.5	5.3	42	17	2.0	5.2	44	0.54	17	1.6
Chl *a* ($\mu g \cdot L^{-1}$)	CHLA	21	4.6	2.0	57	18	3.4	2.0	76	0.67	19	2.7
NH_4^+ ($\mu g \cdot L^{-1}$)	NH_4	136	90	6.4	1271	35	8.3	2.5	149	0.27	72	34
NO_3^- ($\mu g \cdot L^{-1}$)	NO_3	11	6.7	1.1	99	5.5	0.6	1.1	13	0.38	7.7	2.5
DIN ($\mu g \cdot L^{-1}$)	DIN	148	92	7.5	1281	40	8.6	5.2	154	0.26	80	34
TDN ($\mu g \cdot L^{-1}$)	TDN	858	123	373	2177	899	90	212	2129	0.79	884	72
TN ($\mu g \cdot L^{-1}$)	TN	1227	194	604	3297	1208	126	279	2825	0.94	1215	106
TN:TP	TN:TP	23	2.1	13	38	26	2.0	8.1	39	0.30	25	1.5
SO_4^{2-} ($mg \cdot L^{-1}$)	SO_4	4.2	2.2	0.2	25	7.2	3.1	0.1	74	0.44	6.0	2.1
Cl^- ($mg \cdot L^{-1}$)	Cl	0.3	0.03	0.1	0.6	1.5	0.8	0.1	20	0.18	1.0	0.5
Na^+ ($mg \cdot L^{-1}$)	Na	2.4	0.7	0.3	8.8	10	4.6	1.0	113	0.09	6.3	2.3
DOC ($mg \cdot L^{-1}$)	DOC	20	2.1	10	33	15	1.0	10	29	0.05	17	1.1
Extinction coefficient (m^{-1}), base e	ϵ	3.8	0.5	1.3	8.7	2.3	0.3	0.9	5.9	0.02	2.9	0.3
Colour ($mg \cdot L^{-1}$ Pt)	COL	186	29	29	358	38	5.2	8.0	125	<0.001	92	16
Alkalinity ($mg \cdot L^{-1}$)	ALK	28	8.4	2.9	95	110	14	40	389	<0.001	80	11
HCO_3^- ($mg \cdot L^{-1}$)	HCO_3	34	10	3.6	116	125	15	49	379	<0.001	91	12
pH	pH	5.7	—	4.9	7.4	7.6	—	6.9	8.7	<0.001	7.3	—
Si ($\mu g \cdot L^{-1}$)	Si	703	194	40	2750	1563	235	56	4383	<0.001	1246	177
Ca^{2+} ($mg \cdot L^{-1}$)	Ca	10	3.2	0.9	37	24	1.9	10	52	<0.001	19	2.0
Mg^{2+} ($mg \cdot L^{-1}$)	Mg	2.3	0.6	0.3	7.1	11	1.7	3.7	48	<0.001	7.4	1.2
K^+ ($mg \cdot L^{-1}$)	K	0.6	0.2	0.2	2.4	3.6	0.5	0.7	11	<0.001	2.3	0.3
Conductivity ($\mu S \cdot cm^{-1}$)	COND	80	23	11	271	265	33	100	910	<0.001	197	27

Note: Data consist of independent annual estimates collected during the study period (1996–1998) or are from Mitchell and Prepas (1990). Water quality parameters in wetland- and upland-dominated systems were compared with two-tailed t tests; probabilities (P) are included. SE, ± 1 standard error; Min., minimum; Max., maximum. Extinction coefficient data were unavailable for N37 (1997 only), Narrow, Sauer, Long, and Moore lakes. TP, total phosphorus; TDP, total dissolved phosphorus; DIN, dissolved inorganic nitrogen; TDN, total dissolved nitrogen; TN, total nitrogen; DOC, dissolved organic carbon.

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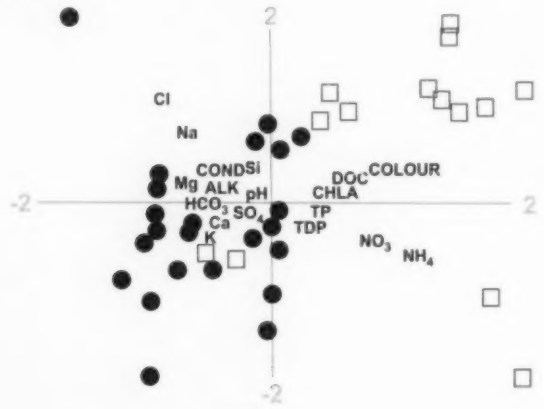
Fig. 2. Biplot of 26 lakes (19 upland lakes (14 for 1 year, 5 for 2 years) and 7 wetland lakes (all for 2 years) for an overall total of 38 observations) based on indirect gradient analysis of lake water chemistry. The contribution of individual water chemistry parameters to the two major ordination axes are superimposed. Lakes in wetland-dominated catchments are identified with open squares, lakes in upland catchments with solid circles. COND, conductivity; ALK, alkalinity; DOC, dissolved organic carbon; CHLA, chlorophyll *a*; TP, total phosphorus; TDP, total dissolved phosphorus.



(Dillon et al. 1991). The connection, although weaker than for TP, between watershed variables and lake TN concentrations is strongest in wetland-dominated systems. Denitrification and other in situ processes related to mean depth were the dominant forces controlling nitrogen concentration in lakes in upland-dominated watersheds.

Phytoplankton

Mean summer Chl *a* concentrations covered 1.5 orders of magnitude (Table 3), and as expected, TP and TN concentrations were the best overall predictors of Chl *a* ($r^2 = 0.70$ and 0.43, respectively, $P << 0.01$). The Chl *a*–TP relationship did not vary detectably among the combined wetland- and upland-dominated data sets and was not enhanced by the addition of other independent variables. Total phytoplankton biomass (BIOM) was most closely related to TP concentration in both wetland- and upland-dominated systems, but these relationships were weaker than those for Chl *a* ($r^2 =$ 0.42 and 0.52, respectively). In a survey of 208 temperate upland-dominated lakes, Chl *a* and mean depth were inversely related ($r = -0.60$; Duarte and Kalff 1989). We found a similar relationship within our upland-dominated systems ($r = -0.63$, $P < 0.001$) but not within our wetland-dominated systems ($P > 0.6$), which may be related to higher colour and, consequently, reduced light penetration in the latter systems (Table 3).

Cyanobacteria were the dominant phytoplankton in all study lakes, followed by Peridineae and Cryptophyceae within wetland- and upland-dominated systems, respectively (Fig. 4*a*). Within wetland-dominated systems, Chlorophyta and Chrysophyceae were equally represented according to percentage phytoplankton composition, but Chrysophyceae were more prevalent than Chlorophyta in upland-dominated systems (Fig. 4*a*). Diatoms were scarce during the July–September study period relative to lakes on the Boreal Shield (Planas et al. 2000). We detected no differences in total phytoplankton biomasses between wetland- and upland-dominated systems, but Chlorophyta and Peridineae biomasses were higher in wetland-dominated systems than in upland-dominated ones (Fig. 4*b*) and compared with data collected on other lakes in the region (Mitchell and Prepas 1990). Cryptophyceae were relatively more abundant in upland- than in wetland-dominated systems (Fig. 4*a*). In contrast, higher Chlorophyta biomasses in wetland- than in upland-dominated systems, despite equivalent TP concentrations, may coincide with greater DIN availability in the former. This is consistent with the observed patterns in DIN and our original hypothesis that N-dependent Chlorophyta would be higher in lakes in wetland-dominated drainages than in upland-dominated ones.

Although total cyanobacterial biomasses were similar, absolute and relative biomasses of Oscillatoriales were greater in upland- than in wetland-dominated systems (Fig. 5). Oscillatoriales are also abundant in other upland-dominated systems in northern Alberta (Prepas and Planas, unpublished data). *Microcystis* spp. was positively linked to NO_3 concentrations in wetland-dominated systems ($r^2 = 0.61$, $P << 0.01$) as were, to a lesser extent, non-nitrogen-fixing Cyanobacteria as a group ($r^2 = 0.29$, $P < 0.05$). Of all the groupings we reviewed, biomass of *Microcystis* spp. was most strongly associated with TP concentrations particularly in wetland-dominated systems ($r^2 = 0.71$, $P << 0.1$).

Relationships between Cryptophyceae biomass (CRYTO) and NH_4 and DOC concentrations in wetland-dominated systems were suggestive of quadratic and linear functions, respectively (Fig. 6). Some Cryptophyceae species are mixotrophic and may prey on bacteria (Tranvik et al. 1989). In wetland-dominated systems, Cryptophyceae may be more dependent on heterotrophy rather than on autotrophy, because higher concentrations of coloured DOC and poorer light than in upland-dominated systems could limit photosynthesis. If bacterivory is the dominant source of energy for Cryptophyceae, the relationship between their biomass and DOC and NH_4 could be indirect, via their prey, the bacteria. Bacteria were not quantified in this study, but their dependence on DOC and competition with phytoplankton for nutrients are well known (e.g., Currie and Kalff 1984).

Cryptophyceae biomass was linearly related to TP and TDP concentrations in upland-dominated systems ($r^2 = 0.53$, $P << 0.01$). Peridineae biomass was either poorly or negatively associated with euphotic-zone nutrients (NO_3, TP, dissolved inorganic carbon (DIC), wetland only $P < 0.05$). Many species of Peridineae can accumulate nutrients below the euphotic zone through diel migration, perhaps as a strategy to reduce interspecific competition (James et al. 1992). Similarly, a negative relationship between Oscillatoriales biomasses and NH_4 concentrations within upland-dominated systems ($r^2 = 0.25$, $P < 0.05$) suggests that non-N_2-fixing Cyanobacteria like Oscillatoriales are inferior competitors compared with N_2-fixing taxa.

Colour, DOC, and wetland coverage

Colour concentrations are dependent on dissolved humic matter and negatively influence underwater light penetration,

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Table 4. Drainage basin and lake morphometry summary data for the 26 study lakes.

		Wetland-dominated (n = 7)				Upland-dominated (n = 19)					Total (n = 26)	
Parameter	Abbreviation	Mean	SE	Min.	Max.	Mean	SE	Min.	Max.	P	Mean	SE
Catchment area (km^2)	CA	9.41	2.82	0.75	20.42	12.28	4.78	0.58	88.24	0.61	11.51	3.55
Drainage basin area (km^2)	DBA	8.27	2.64	0.56	18.80	10.88	4.36	0.49	82.40	0.61	10.18	3.24
Effective DBA (km^2)	eDBA	6.30	1.15	2.63	15.88	2.46	0.52	0.10	9.45	0.007	4.04	0.65
Slope (%)	SLOPE	1.1	0.5	0.3	3.9	4.1	0.5	1.1	11	< 0.001	3.3	0.5
Upland conifer (% of DBA)	CONIF	21	6.7	0	43	17	2.8	1.2	42	0.53	18	2.7
Upland deciduous (% of DBA)	DECID	3.1	2.8	0	20	64	4.0	30	85	< 0.001	47	6.1
Wetlands (% of DBA)	WETL	76	7.1	57	100	17	2.3	0	44	< 0.001	33	5.8
Bogs (% of DBA)	BOG	44	11	11	85	2.4	1.1	0	20	< 0.001	14	4.7
Total fens (% of DBA)	FEN	30	5.6	7.8	45	8.8	1.9	0	30	< 0.001	15	2.7
Rich fens (% of DBA)	RFEN	12	6.8	0	39	8.8	1.9	0	30	0.56	9.8	2.2
Poor fens (% of DBA)	PFEN	17	7.3	0	45	0.01	0.01	0	0.2	0.004	4.7	2.4
Swamps & marshes (% of DBA)	SWAMP	1.9	1.0	0	7.0	5.4	0.9	0	12	0.003	4.4	0.7
Lake elevation (m)	ELEV	613	36	505	730	633	11	549	740	0.44	625	12.5
Lake area (km^2)	LA	1.15	0.24	0.19	2.00	1.40	0.53	0.09	9.28	0.67	1.33	0.39
Mean depth (m)	Z_{mean}	1.3	0.3	0.7	2.5	3.8	0.7	0.9	14	0.004	3.1	0.6
Maximum depth (m)	Z_{max}	3.1	0.7	1.8	5.8	8.5	2.0	1.8	38	0.02	7.1	1.6
Lake volume ($m^3 \times 10^6$)	LV	1.80	0.70	0.19	5.72	7.94	4.19	0.27	77.40	0.17	6.29	3.09
Water residence time (years)	τ	0.5	0.2	0.1	2.3	10.8	5.7	0.2	100	0.08	7.0	3.65
Drainage basin area/lake volume	DBA/LV	6.48	2.49	1.28	19.66	3.86	0.91	0.44	16.7	0.35	4.56	0.94
Effective DBA/lake volume	eDBA/LV	6.68	1.41	0.58	18.34	2.29	0.51	0.13	7.65	0.01	4.10	0.74
Drainage basin area/lake area	DBA/LA	6.69	1.66	1.86	13.21	9.30	1.19	1.52	21.42	0.23	8.60	0.99
Catchment area/lake volume	CA/LV	7.36	2.59	1.96	21.15	4.27	0.96	0.51	17.84	0.30	5.11	1.00

Note: Data are from this study and from Mitchell and Prepas (1990). Physical parameters in wetland- and upland-dominated systems were compared with two-tailed t tests; probabilities (P) are included; SE, ±1 standard error; Min., minimum; Max., maximum. Data for eDBA, eDBA/LV, and τ consist of independent annual estimates collected during 1996 and 1997 or were taken from Mitchell and Prepas (1990). Other parameters were assumed constant over the study period (1996–1998). eDBA and eDBA/LV were unavailable for Narrow, Sauer, Long, and Moore lakes.

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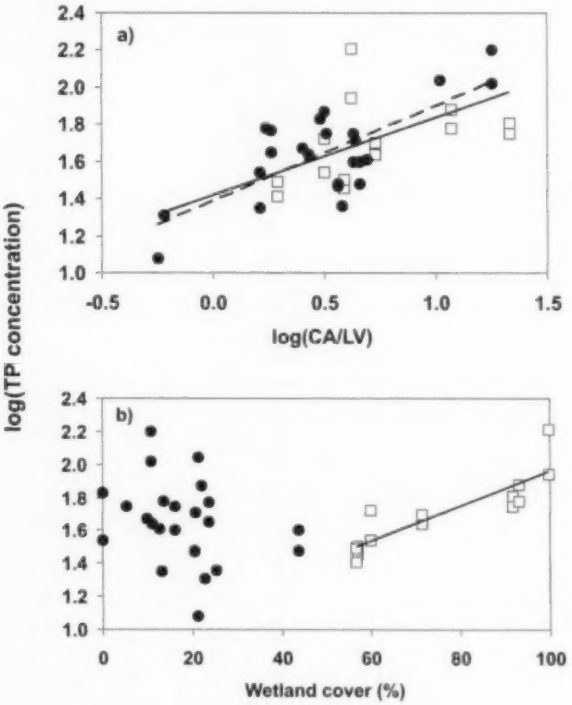
Fig. 3. Relationships between mean July–September euphotic total phosphorus (TP) concentration and (*a*) catchment area/lake volume (CA/LV) (solid line, all systems, $r^2 = 0.42$, $P < 0.001$; broken line, upland systems, $r^2 = 0.56$) and (*b*) percentage wetland cover ($r^2 = 0.78$, $P < 0.001$) in Boreal Plain wetland- and upland-dominated systems. Open squares, wetland-dominated systems ($n = 14$ independent estimates from 7 lakes); solid circles, upland-dominated systems ($n = 24$ independent estimates from 19 lakes).



limiting colonization depths for primary producers (Chambers and Prepas 1988). Colour was strongly associated with wetland and bog and less so with fen cover in the combined data set ($r = 0.81$, 0.78 ($P << 0.01$), and 0.44 ($P < 0.05$), respectively). In contrast to relationships with TP, TN, and DOC, eDBA/LV was more strongly linked with colour (COL) than CA/LV and DBA/LV ($r = 0.80$, 0.69, and 0.64, respectively); eDBA/LV combined with drainage basin slope (SLOPE) explained 71% of colour variability (eq. 9). Colour also coincided negatively with water residence time ($r = -0.84$), which is consistent with in-lake degradation of humic matter (Rasmussen et al. 1989).

$$\text{(9)} \quad \text{ALL: } \log(\text{COL}) = 1.84 + 0.47\log(\text{eDBA/LV})^{**} - 0.06\text{SLOPE}^{**},\ r^2 = 0.71$$

The drainage basin slope in eq. 9 could represent the transition from organic peatlands towards mineral soils, which export less humic matter, or distinct drainage patterns between upland- and wetland-dominated watersheds. Although catchment slopes are low in our study (≤11%), they explained one-quarter of colour variability as a single predictor. Based on a study focused on the Precambrian Shield in Labrador, Rasmussen et al. (1989) interpreted the absence of a relationship between colour and wetland cover as due to the overriding influence of slope. In the Labrador study and peatland-dominated subarctic plateau (McEachern et al. 2000), DOC and colour were highly correlated ($r^2 = 0.86$ and 0.89, respectively), whereas in our study, the relationship was much weaker ($r^2 = 0.48$). Much of the DOC in Boreal Plain lakes may be produced in situ (Curtis and Prepas 1993). As expected, within the combined data set, colour and Chl *a* concentration accounted for most of the variabil-

Fig. 4. Mean July–September euphotic biomasses of dominant phytoplankton taxa within the 22 Boreal Plain wetland- and upland-dominated systems surveyed during 1996 and 1997 compared as (*a*) relative and (*b*) absolute values. Summer means for 1996 and 1997 were averaged. Different letters over bars signify significant ($P < 0.05$) differences within a taxon between wetland-dominated (open bars) and upland-dominated (solid bars) systems. Cyano, Cyanobacteria; Crypto, Cryptophyceae; Diato, Diatoms; Eugleno, Euglenophyceae; Peridi, Peridineae; Chloro, Chlorophyta; Chryso, Chrysophyceae.

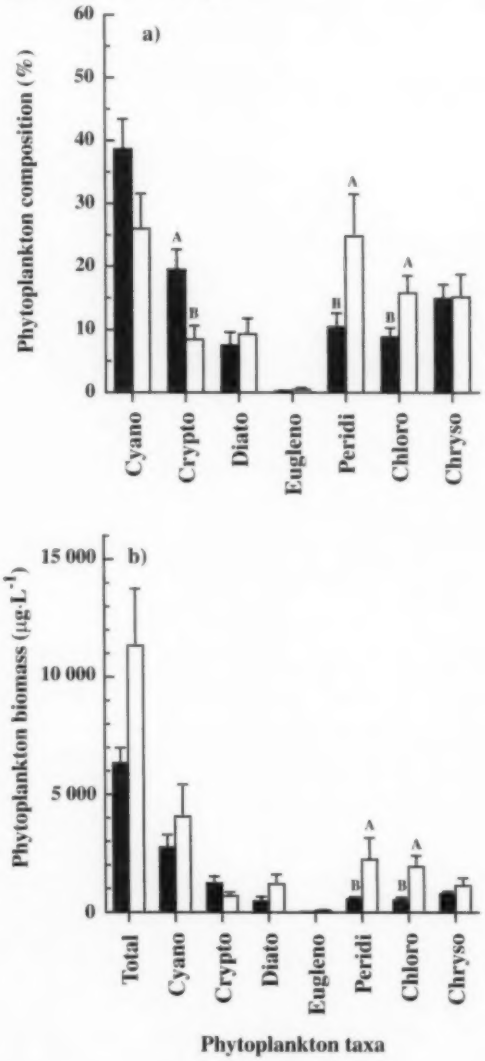


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Fig. 5. Summer (July–September) cyanobacterial biomasses within the 22 Boreal Plain wetland- and upland-dominated systems surveyed during 1996 and 1997 compared as (*a*) relative and (*b*) absolute values. Summer means for 1996 and 1997 were averaged. For each graph, total cyanobacterial biomass is depicted by major taxa (Microcys, *Microcystis* spp.; Chroococ, Chroococcales; Nostoc, Nostocales; Oscillat, Oscillatoriales). Different letters over bars signify significant ($P < 0.05$) differences within a taxon between wetland-dominated (open bars) and upland-dominated (solid bars) systems.

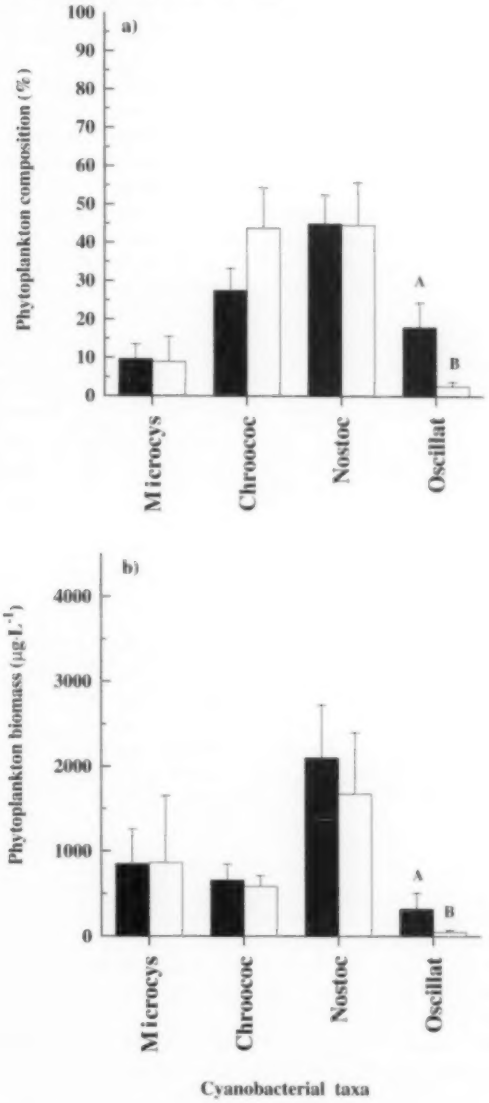
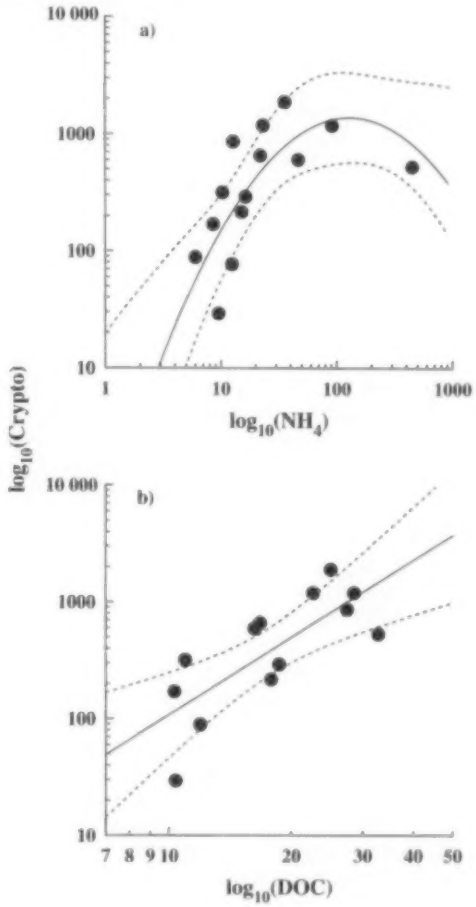


Fig. 6. Relationships between mean summer (July–September) Cryptophyceae (Crypto) biomass and (*a*) ammonia (NH_4^+) and (*b*) dissolved organic carbon (DOC) concentrations within the seven Boreal Plain wetland-dominated systems surveyed during 1996 and 1997. Broken lines represent 95% confidence intervals. WETLAND: $\log(\text{CRYPTO}) = -1.01 + 4.18\log(NH_4)^{**} - 1.05(\log(NH_4))^{2**}$, $r^2 = 0.59$.



ity in light extinction ($r^2 = 0.80$, $P << 0.01$). As predicted, wetland (primarily bog) coverage in the drainage, along with the variable eDBA/LV, were strongly associated with colour concentrations in all our lake water.

Studies based in Labrador, Finland, and northern Alberta with relatively high wetland coverage (up to 25%, 58%, and 85%, respectively) noted strong relationships between wetland coverage and in-lake organic carbon concentrations (Engstrom 1987; Kortelainen 1993; Halsey et al. 1997). Although DBA/LA explained up to 70% of DOC variability in the peatland-dominated systems of the Caribou Mountains (McEachern et al. 2000), DOC concentrations in our combined data set were positively associated with percentage wetland cover and CA/LV, but relationships were relatively weak given the strong autochthonous input ($r^2 = 0.32$ and 0.28, respectively). In upland-dominated systems, CA/LV and mean depth explained 21% and 38% of DOC variability, respectively. In contrast, in the wetland-dominated subset, percentage wetland cover and eDBA explained considerably more DOC variability ($r^2 = 0.74$ and 0.64, respectively), whereas CA/LV explained 27% of DOC variability.

Engstrom (1987) predicted that DOC and water residence time are strongly related in systems where DBA/LA is > 4. In our study, DOC was inversely related to water residence

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time (r = –0.46) and not detectably related to DBA/LA (mean = 8.0). DOC concentration and watershed slope were weakly related (r^2 = 0.16, P < 0.02), whereas this relationship was much stronger (r^2 = 0.40) in lakes on the Boreal Shield (D'Arcy and Carignan 1997). In sharp contrast to colour, the connection between vegetative cover and DOC concentrations in lakewater on the Boreal Plain was stronger in wetland-dominated drainages than in upland-dominated ones. In situ generation of DOC was likely the prevailing force in upland-dominated drainages.

Effective drainage basin area as a predictor

Mean water residence time (τ) was more than 20-fold longer for upland-dominated lakes than for wetland-dominated ones (11 and 0.5 years, respectively; Table 4), attributable to the deeper lake basins and smaller eDBAs within the upland-dominated systems. Positive associations (r = 0.65) between lakewater residence time and alkalinity, conductivity, HCO_3^-, Mg^{2+}, and K^+ suggest the influence of hydrologic setting, specifically lake flushing rates for some but not all dominant ions. Differences between estimated isotopically defined eDBA and topographically defined DBA were less pronounced within wetland-dominated catchments compared with upland-dominated catchments. On average, wetland- and upland-dominated eDBAs were about three-quarters and one-quarter of the DBA, respectively (Table 4), the former reflecting a relatively higher wetted fraction or contributing area within the drainage basin and the latter reflecting lower overall runoff contributions from upland areas consistent with loss to groundwater. Within the 26-lake data set, runoff (R from eq. 3) was positively related to bog area (r^2 = 0.87; P < 0.001) but was not detectably linked with DBA, suggesting that bogs play a key role in influencing surface runoff in our study region.

eDBA is positively related to colour and percentage bog cover (r^2 = 0.40 and 0.37, respectively, P < 0.001) and negatively related to drainage basin slope and percentage upland cover (r^2 = 0.30 and 0.47, respectively, P < 0.001). In wetland-dominated lakes, eDBA is a stronger correlate with DOC and TN than with DBA. Within the whole data set, eDBA was more strongly associated with lakewater colour than DBA, suggesting a connection with colour-producing wetlands.

In conclusion, this study found that bogs release more phosphorus than other vegetation categories, and rich fens appear to sequester more phosphorus and nitrogen than other vegetation categories in undisturbed lakes on the Boreal Plain. In upland-dominated lakes, the relative size of the watershed (DBA/LV) was the strongest predictive factor for TP concentration. In contrast, lakewater colour concentration was strongly linked to the wetland connectivity parameter eDBA/LV. In situ nitrogen concentrations were positively linked to percentage wetland cover. Phytoplankton community composition in these lakes was consistent with greater availability of inorganic nitrogen in the lakes with wetland-dominated catchments.

Acknowledgements

Funding was provided by Sustainable Forest Management Network (SFMN; NSERC/SSHRC) grants to E. Prepas, W. Tonn, C. Paszkowski, and T. Prowse. Additional funding was provided from the Natural Sciences and Engineering Research Council (NSERC) research grants to E. Prepas and D. Planas. E. Allen, R. Bennett, C. Blanchard, T. Charette, K. Gibson, B. Gingras, M. Holst, S. Manchur, D. Millions, C. Nahorniak, and K. Westcott assisted with data analyses and manuscript preparation. B. Pinel-Alloul, P. D'Arcy, and K. Webster commented on earlier drafts of the manuscript. The concept of comparable surveys of land–aquatic interactions on the Boreal Plain and Shield were first discussed with B. Pinel-Alloul, R. Carignan, R. Peters, Y. Prairie, and P. Magnan. Data for this project were contributed in part by the Terrestrial and Riparian Organisms, Lakes and Streams (TROLS) project, supported by an NSERC Co-operative Special Projects grant to E. Prepas (Prepas et al. 2001). We acknowledge support by Ainsworth Lumber Company Ltd., Alberta Economic Development and Tourism, Alberta Environmental Protection, Alberta-Pacific Forest Industries Ltd., Daishowa-Marubeni International Ltd., Manning Diversified Forest Products, National Research Council of Canada Industrial Research Assistantship Program, Syncrude Canada Ltd., and Weyerhaeuser Canada Ltd. Air transportation was supplied by B. Allison Flying Services, Slave Air, and Voyage Air. Research was based out of the Meanook Biological Research Station. This manuscript was prepared while the senior author was a visiting researcher at the Centre de Recherche en Géochimie Isotopique et en Géochronologie (GEOTOP; Université du Québec à Montréal) and the Groupe de Recherche Interuniversitaire en Limnologie (GRIL; Université de Montréal).

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Effects of individual quotas on catching efficiency and spawning potential in the Alaska sablefish fishery

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Abstract: Individual fishery quota (IFQ) management eliminates the race for fish and may improve economic efficiency, conservation, and safety in fisheries. Empirical information documenting these effects is limited, even though IFQs have been used since the late 1970s. We analyzed fishery data from the Alaska sablefish (*Anoplopoma fimbria*) longline fishery, which came under IFQ management in 1995. We compared the fishery data with fishery-independent survey data, which acted as a control to separate annual changes in population demographics from changes due to IFQ management. We found that IFQ management increased fishery catch rate and decreased harvest of immature fish. Catching efficiency increased 1.8 times with the change from an open-access to an IFQ fishery. The improved catching efficiency of the IFQ fishery reduced variable costs to catch the quota from 8 to 5% of landed value, a savings averaging $3.1 million US annually. Decreased harvest of immature fish improved the chance that individual fish will reproduce at least once. Spawning potential of sablefish, expressed as spawning biomass per recruit, increased 9% for the IFQ fishery. Switching from the open-access fishery's race for fish to IFQs provided two clear benefits that should be considered when evaluating management options for other open-access fisheries.

Résumé : La gestion des pêches commerciales à l'aide de quotas individuels (IFQ) élimine la compétition pour les poissons et peut probablement augmenter l'efficacité économique, la conservation et la sécurité de la pêche. Il y a peu de données empiriques sur ces effets, bien que les IFQ soient en usage depuis la fin des années 1970. Nous analysons ici les statistiques de la pêche à la palangre de la Morue charbonnière (*Anoplopoma fimbria*) en Alaska qui est gérée à l'aide d'IFQ depuis 1995. Une comparaison des données provenant de la pêche commerciale avec celles d'autres inventaires indépendants de la pêche et utilisées comme témoins a permis de séparer les effets de la gestion par IFQ des changements démographiques annuels de la population. Il ressort de ces analyses que la gestion par IFQ augmente les taux de capture de la pêche et décroît la prise de poissons immatures. L'efficacité de la capture a augmenté d'un facteur de 1,8 lorsque l'accès libre a été remplacé par les quotas individuels. Cette augmentation d'efficacité a réduit les frais variables reliés à l'atteinte des quotas de 8 à 5% de la valeur des poissons débarqués, une économie de 3,1 millions $US chaque année. La diminution de la récolte de poissons immatures augmente la probabilité que chaque poisson se reproduise au moins une fois. Le potentiel de fraye de la Morue charbonnière, défini comme la biomasse des géniteurs par recrue, a augmenté de 9%. Le remplacement d'une pêche à accès libre qui entraîne une compétition pour les poissons par une pêche gérée par IFQ produit donc deux bénéfices nets qui doivent être pris en compte lorsqu'on évalue les options de gestion dans un pêche commerciale à accès libre.

[Traduit par la Rédaction]

Introduction

Groundfish fisheries in Alaska are managed by annual catch quotas, limited access, bycatch measures including catch limits, and closed areas triggered by reaching these limits. Since 1995, the sablefish (*Anoplopoma fimbria*) and Pacific halibut (*Hippoglossus stenolepis*) longline fisheries also have been managed by individual (fishery) quotas or IFQs. An annual catch quota sets the overall level of harvest, whereas an individual quota allocates the quota among individual fishermen. The Magnuson–Stevens Act defines an IFQ as "a Federal permit under a limited access system to harvest a quantity of fish, expressed by a unit or units representing a percentage of the total allowable catch of a fishery that may be received or held for exclusive use by a person."

IFQs have been used in some countries since the late 1970s and in a few fisheries in the United States since 1983 (National Research Council (NRC) 1999; Wertheimer and Swanson 1999). Their purpose is to address problems of common property fisheries where individual ownership is not assigned, eliminating the race for fish and improving economic efficiency, conservation, and safety (NRC 1999). The North Pacific Fishery Management Council considered IFQs for sablefish and halibut longline fisheries due to allocation and gear conflicts, ghost fishing of lost gear, discard mortality, product quality, and safety (NRC 1999).

Some empirical information exists on the economic, con-

Received May 17, 2000. Accepted March 28, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca. on June 4, 2001.
J15772

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 DOI: 10.1139/cjfas-58-7-1300 © 2001 NRC Canada

servation, and safety effects of IFQs. These effects include nearly year-round availability of fresh rather than frozen fish, increased ex-vessel value, and reduced crew sizes (Casey et al. 1995), less lost and abandoned gear and reduced fishing mortality from lost and abandoned gear (NRC 1999), reduced quota overages (NRC 1999, table G.2), reduced discard of bycatch (NRC 1999), increased management and enforcement costs (NRC 1999), changes in fleet behavior (Sullivan and Rebert 1998), and reduced search and rescue missions (NRC 1999, table 3.3).

Our analysis focuses on catching efficiency and spawning potential in the Alaska sablefish fishery; our purpose was to examine how IFQ management affected these two aspects of the fishery rather than to conduct an overall evaluation of sablefish IFQ management. We describe two benefits of IFQ management for sablefish, an increase in fishery catch rates and a decrease in the fraction of immature fish captured, which coincided with the switch from open-access to IFQ management. We compare fishery data from before and after inception of IFQ management to fisheries-independent survey data collected through the same time period. The survey data in effect provide for a controlled experiment to separate annual changes in population demographics from changes due to IFQ management. We further analyze the fishery data to determine what changes in fishing practices lead to these benefits.

Alaska sablefish longline fishery

Sablefish have been exploited since the end of the nineteenth century by U.S. and Canadian longline fishermen, developing as a secondary activity of the halibut longline fishery of the United States and Canada. Catches were relatively small, averaging 1700 metric tons (t) from 1930 to 1957, and generally limited to areas near fishing ports (Low et al. 1976). Japanese longliners began operations in the eastern Bering Sea in 1958 and in a few years shifted to the Aleutian Islands region and Gulf of Alaska after their fishing grounds in the eastern Bering were preempted by expanding Japanese trawl fisheries. Catches peaked at over 50 000 t in 1972 (Low et al. 1976), but the heavy fishing by foreign vessels led to a substantial population decline and fishery regulations that reduced catches to about one fifth of their peak (Sigler et al. 1999). The U.S. longline fishery began expanding in 1982 in the Gulf of Alaska and in 1988 harvested all sablefish taken in Alaska except minor joint venture catches. The expansion of the U.S. fishery during the 1980s was helped by exceptional recruitment during the late 1970s (Sigler et al. 1999). This exceptional recruitment fueled an increase in abundance for the population that had been depleted by the heavy fishing during the 1970s. Increased abundance led to relaxation of fishing quotas and catches peaked again in 1988, following the first peak in 1972. Abundance and catches have since fallen, as the exceptional late 1970s year-classes have died off, and in 1998, catches were about 37% of the 1988 peak (Sigler et al. 1999).

Most (~88% from 1995 to 1998) sablefish were caught by longline (Sigler et al. 1999). Some (~12%) were caught as bycatch during directed trawl fisheries for other species groups such as rockfish and deepwater flatfish, and less than 1% were caught by pots. Only the longline fishery is part of the IFQ program. Catches in the United States Exclusive Economic Zone (U.S. EEZ), the area inside the IFQ program, averaged 25 000 t per year from 1985 to 1998 and 17 000 t per year from 1995 to 1998. Five Alaska state fisheries that are not part of the IFQ program also land sablefish, averaging 3000 t per year from 1985 to 1998.

Season length began to decrease after the change from a primarily foreign fishery to a completely domestic fishery. The year-round season in the Gulf of Alaska, the area responsible for the majority of the catches, became progressively shorter beginning in 1984 (Table 1). By the late 1980s, the race for fish caused season length to decrease to 1 or 2 months (the season was closed once the quota was reached in the open-access fishery). In some areas, this open-access fishery was as short as 9 days, warranting the label "derby" fishery. For example, from 1984 to 1987, the season length decreased from 8 months to less than 2 weeks as the number of vessels increased fivefold in the West Yakutat region (NRC 1999, fig. 1.1B). Season length continued to decrease until IFQs were implemented in 1995. Under IFQ management, the season was set at 8 months.

Predicting when to close the open-access fishery was difficult because of the speed and brevity of the fishery. Often the initial open period was followed by a "mop-up" fishery if the quota had not been reached in the initial open period. The sablefish quota frequently was exceeded in the Gulf of Alaska (Table 2). In contrast, the sablefish quota has never been exceeded during IFQ management. The halibut quota also was exceeded frequently during the open-access fishery but not during the IFQ fishery (NRC 1999, table G.2).

Sablefish biology

Sablefish inhabit the northeastern Pacific Ocean from northern Mexico to the Gulf of Alaska, westward into the Aleutian Islands, and into the Bering Sea (Wolotira et al. 1993). Adult sablefish occur along the upper continental slope, in gullies that cross the continental shelf (cross-shelf gullies), and in deep fjords, generally at depths greater than 200 m. Sablefish appear to form two populations, a northern or Alaska population and a southern or west coast population, with mixing of the two populations occurring off southwest Vancouver Island and northwest Washington (Kimura et al. 1998). Alaska sablefish are highly migratory for at least part of their life, and substantial movement has been documented (Heifetz and Fujioka 1991; Kimura et al. 1998). Sablefish are a long-lived demersal species; ages over 40 years commonly are recorded (Kimura et al. 1993). Sablefish grow rapidly in early life, reaching average maximum lengths and weights of 69 cm and 3.4 kg for males and 82 cm and 6.1 kg for females. Fifty percent of females are mature at 65 cm, while 50% of males are mature at 57 cm (Sasaki 1985), corresponding to ages of 6.5 years for females and 5 years for males.

Data sources and methods

Catch, effort, and length data were collected at sea during commercial fishing operations and during fisheries-independent longline surveys. Catch per hook was computed from the catch and effort data. The mature fraction of the catch was computed from the length data. The computed values of survey and fishery catch per hook were compared during the open-access and IFQ fisheries to determine if IFQ fishery efficiency was higher. Mature fraction values also were compared to determine if fewer immature fish

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Table 1. Season length (days) by region and year, 1983–1998.

Year	Bering Sea	Aleutian Islands	Western	Central	West Yakutat	East Yakutat/Southeast
1983	365	365	365	365	365	222
1984	366	366	366	255	245	181
1985	365	247	176	143	135	111
1986	na	na	94	56	40	17
1987	266	227	69	59	15	9
1988	366	163	99	73	32	32
1989	211	36	104	57	17	17
1990	365	214	92	59	16	20
1991	365	365	55	34	27	11
1992	237	289	83	20	16	9
1993	301	365	21	20	16	10
1994	220	220	11	11	11	11
1995	319	319	319	319	319	319
1996	319	319	319	319	319	319
1997	319	319	319	319	319	319
1998	319	319	319	319	319	319

Note: The Western, Central, West Yakutat, and East Yakutat/Southeast regions are located in the Gulf of Alaska. na, not available.

Table 2. Frequency and magnitude of sablefish overharvests in the Gulf of Alaska, 1985–1998 (National Marine Fisheries Service, Alaska Regional Office, Juneau, Alaska).

Year	Frequency (%)	Average overharvest (%)
1985–1994	75	5
1995–1998	0	–9

were caught during the IFQ fishery. A detailed description of data sources and methods follows.

Fishery

From 1990 to 1998, at-sea fishery observers recorded data from 16 133 longline sets targeting sablefish, averaging 4800 hooks per set. Catch, effort, and length data were collected. Observers only collected length data from the predominant species in a set. Observers collected length data before catch sorting so discarding would not affect length samples. A set was defined as targeting sablefish where sablefish were at least 50% of the catch by weight. Fishermen also recorded catch and effort but no length data for 538 longline sets targeting sablefish through a voluntary sablefish logbook program initiated in 1997. The latter program collected data from smaller boats not required to carry an observer.

The logbook reported weights usually are approximate because vessel captains typically estimated and recorded catch for each set in the logbook while at sea and without an accurate scale measurement. An accurate weight for the entire trip was measured at landing and recorded as the IFQ landing report. We adjusted the captain's estimate of catch per set using the ratio of IFQ landing report and logbook reported weight.

The fishery catch rates were standardized to account for differences in hook spacing. Hook spacings of about 1 m (reported spacings of 39 in. and 42 in.) were the most common spacings used in the directed sablefish longline fishery, accounting for 64% of all observed sets from 1990 to 1998. We chose the 1-m spacing as the standard, a spacing that we have tested in sablefish hook spacing experiments. Two hook spacing experiments have been conducted, one from 4 to 13 July 1986 in Chatham Strait, Alaska, and the other from 25 to 26 July 1999 in the Gulf of Alaska off Icy Bay, Alaska. In the first experiment, three hook spacings were tested, 1, 2, and 4 m, and in the second experiment, a fourth spacing of 0.5 m was added. All hook spacings were tested in each set to account for the effect of set location on the resultant catch rates. The order of hook spacing within a set was varied systematically to control for interaction effects of treatments on catch rate. Circle hooks (size equivalent to 13/0) were used in both experiments; they were baited with herring in the first experiment and with squid in the second experiment. For both experiments, catch per hook increased as hook spacing increased (Table 3).

Skud and Hamley (1978) developed a method for standardizing halibut longline catch rates for hook spacing. This method continues to be applied by the International Pacific Halibut Commission (Sullivan et al. 1999). The Commission analysts used an asymptotic function, $CPUE_h/CPUE_s = C_\infty (1 - \exp(-kh))$, where CPUE is catch per hook, h is some hook spacing, s is the standard hook spacing, C_∞ is the maximum relative catch per hook, and k is a measure of how fast this maximum is reached. This equation implies that catch per hook increases with hook spacing but at a rate less than proportional to hook spacing. Parameter estimates from the sablefish hook spacing experiments are $C_\infty = 2.2$ and $k = 0.57$. The estimated asymptote of 2.2 is only slightly larger than the relative catch per hook of 4-m gear. This implies that the relative catch per hook is near maximum at this spacing. The number of standardized hooks N_{std} was computed from the number of unstandardized hooks N_{unstd} for each longline set from the logbook and observer databases, $N_{std} = N_{unstd}2.2(1 - \exp(-0.57h))$, where h is expressed in metres. A standardized CPUE was calculated for each set by dividing the weight of the catch by the standardized number of hooks, $CPUE_{std} = \text{weight}/N_{std}$.

The standardized catch rates by set were used to compute average catch rates by vessel for each North Pacific Fishery Management Council region: Bering Sea, Aleutian Islands, and the Gulf of Alaska regions Western, Central, West Yakutat, and East Yakutat/Southeast. Catch rate by vessel–region was computed by dividing each vessel's total regional catch by its total regional effort. The average for each region was computed from the vessel–region catch rates. These averages combined the observer and logbook data. The averages for the IFQ fishery were computed using only data collected during the summer survey period, which the 8-month long IFQ fishery overlapped. Selecting this subset of the data removes the effect of seasonality on the comparison of the

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Table 3. Sablefish catch (kg) per hook for four different hook spacings.

		Hook spacing (m)			
Year	Set	0.5	1	2	4
1986	1	na	0.62	1.03	1.33
1986	2	na	1.10	1.33	1.40
1986	3	na	0.61	1.13	1.39
1986	4	na	0.92	1.34	1.83
1986	5	na	0.74	1.07	1.58
1986	6	na	0.93	1.00	1.51
1986	7	na	0.73	1.11	1.61
1986	8	na	1.00	1.44	1.72
1986	9	na	1.02	1.56	1.74
1986	10	na	0.92	1.37	2.08
1999	1	0.10	0.09	0.17	0.15
1999	2	0.30	0.43	0.50	0.55
1999	3	0.16	0.08	0.29	0.40
1999	4	0.26	0.43	0.91	1.30
1999	5	0.45	0.68	1.06	1.53
1999	6	0.49	0.74	1.35	1.48

Note: The 0.5-m hook spacing was not tested in 1986. na, not available.

IFQ fishery and survey. This approach cannot be used for comparisons of the open-access fishery and survey because the open-access fishery and survey did not overlap; the open-access fishery occurred during spring, while the survey occurred during summer. Thus, comparisons of the open-access fishery and survey are confounded with seasonality. We tested for seasonality by examining fishery data for the spring and summer from years where seasonal data were available, 1995–1998.

Hook size, which may vary in the commercial fishery, was not considered in our analysis because these data are not collected by the fishery observers. However, typical sablefish and cod hooks are similar in size, so any effect on catch rates and size selectivity should be small. In contrast, typical halibut hooks are about one and one-half (1.5) times larger than typical sablefish hooks. In an experiment comparing these two hook sizes, sablefish catch rates were 33% lower for the larger hooks and sablefish size frequencies were similar (M.F. Sigler, National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratory, Juneau, Alaska, unpublished data). These results imply that fishermen typically will not use halibut hooks to fish for sablefish because of the catch rate reduction.

Longline surveys

Catch, effort, and length data were collected during sablefish longline surveys conducted annually since 1978 (Sasaki 1985; Sigler and Fujioka 1988; Sigler and Zenger 1989). The longline surveys sampled cross-shelf gullies and the upper continental slope. Sampling depths were about 150–1000 m. About 88 standard stations were sampled each year; about 66 of these are located in the usual fishing grounds during the IFQ fishery. The latter stations were selected for comparison with the fishery data. There were 8–16 stations per region. The same number of stations were sampled each year from 1990 to 1998. Each station consisted of 7200 hooks spaced 2 m apart along a groundline 16 km long, except in the Bering Sea, where each station consisted of 8100 hooks along a groundline 18 km long. Only longline surveys conducted from 1990 to 1998 in the Gulf of Alaska, in 1996 and 1998 in the Aleutian Islands, and in 1997 in the eastern Bering Sea were compared with the fishery data. The Bering Sea and Aleutian Islands also were sampled from 1990 to 1994, but with different longline gear. This lack of standard sampling of the Bering Sea and Aleutian Islands for all years from 1990 to 1998 limits our analyses for these regions.

The survey catch data were stratified by depth interval (100-m intervals from 100 to 400 m and 200-m intervals from 400 to 1000 m) to account for differences in catch rate among the surveyed depths, and then, catch rates were computed by set and depth strata. The fishery catch rates were not stratified by depth because the fishery depth information was not detailed enough. The survey catch rates by set–depth were adjusted to the fishery standard of 1-m hook spacing. Average catch rates by depth strata were computed for each management region and then combined across depth strata by weighting each depth–region catch rate by the amount of habitat area in that management region and depth strata. The resultant values were catch rates by management region and year. These habitat-weighted catch rates provide indices of sablefish relative abundance to compare with the fishery catch rates.

Fraction mature

The fraction of the sampled population (numbers) that was mature was computed from length data and prior estimates of maturity at length. A logistic equation was used to represent maturity at length, $1/(1 + e^{-\beta(L-L_{50})})$, where L is length, L_{50} is the length at 50% maturity, and β is the slope at L_{50}; L_{50} is 57 cm for males and 65 cm for females and $\beta = 0.4$ (values estimated from Sasaki 1985, fig. 23).

Distance between sets

The distance between sets is a measure of the crowding on the grounds during the open-access fishery. For each set, we determined the distance to the nearest set by the same vessel. We chose to compare sets by the same vessel for two reasons. First, only part of the fleet is observed and there usually are unobserved vessels fishing nearby the observed vessels. However, the between-set distance for the same vessel measures the influence of these unobserved vessels and the crowding on the grounds. Second, vessels typically record their fishing locations, so they are unlikely to repeat fishing a location, whereas they inadvertently may fish a location previously fished by another vessel that has left the area. We examined fishing locations as far back as the previous 7 days. We chose 7 days as the cutoff because fishermen report that this is the length of time that they typically let the grounds "rest" before returning to an area.

Results

Fishery catch rates

Fishery catch rates increased with the transition from an open-access to an IFQ fishery. Fishery catch rates by region and year averaged 0.24 kg per hook during the open-access fishery and 0.39 kg per hook during the IFQ fishery (during summer) (Table 4). Fishery catch rates increased even though sablefish abundance was decreasing; survey catch rates by region and year averaged 0.56 kg per hook during the open-access fishery and 0.43 kg per hook during the IFQ fishery. We paired the fishery and survey catch rates by region and year and computed the paired differences to control for the effect of abundance changes on the fishery catch rates. These paired differences showed that fishery catch rates averaged 0.31 kg per hook less than survey catch rates during the open-access fishery but only 0.04 kg per hook less than survey catch rates during the IFQ fishery. Fishery catch rates by region and year always were less than the corresponding survey catch rates during the open-access fishery but were similar during the IFQ fishery (Fig. 1). These

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Table 4. Longline survey and longline fishery catch per hook, mature fraction, and fishery season length (months) by region, 1990–1998.

Year	Region	Season length (months)	Survey catch per hook (kg)	Fishery catch per hook (kg)	Survey male fraction mature	Fishery male fraction mature	Survey female fraction mature	Fishery female fraction mature
Open-access fishery								
1990	WGOA	3.0	0.40	0.25	0.80	0.73	0.77	0.52
1990	CGOA	1.9	0.58	0.27	0.87	0.75	0.82	0.60
1990	WYAK	0.5	0.69	0.30	0.84	0.81	0.83	0.68
1990	EYSE	0.6	0.55	0.27	0.81	na	0.80	na
1991	WGOA	1.8	0.33	0.20	0.77	0.81	0.67	0.76
1991	CGOA	1.1	0.54	0.24	0.84	0.71	0.80	0.62
1991	WYAK	0.8	0.74	0.29	0.86	0.75	0.87	0.66
1991	EYSE	0.3	0.75	0.31	0.87	0.84	0.85	0.43
1992	WGOA	2.7	0.15	0.14	0.62	0.85	0.46	0.76
1992	CGOA	0.6	0.48	0.26	0.85	0.80	0.80	0.65
1992	WYAK	0.5	0.81	0.24	0.86	0.85	0.84	0.76
1992	EYSE	0.3	0.67	0.28	0.83	0.78	0.84	0.55
1993	WGOA	0.6	0.38	0.13	0.79	0.56	0.66	0.43
1993	CGOA	0.6	0.54	0.34	0.85	0.78	0.80	0.64
1993	WYAK	0.5	0.78	0.26	0.83	0.81	0.85	0.74
1993	EYSE	0.3	0.63	0.36	0.77	0.79	0.77	0.73
1994	WGOA	0.3	0.29	0.13	0.66	0.60	0.54	0.46
1994	CGOA	0.3	0.51	0.24	0.87	0.78	0.87	0.59
1994	WYAK	0.3	0.71	0.25	0.90	0.85	0.91	0.76
1994	EYSE	0.3	0.61	0.14	0.87	0.95	0.86	0.94
Average			0.56	0.24	0.82	0.78	0.78	0.65
Average paired difference				–0.31		–0.04		–0.13
Average paired ratio				0.47				
IFQ fishery								
1995	WGOA	8.0	0.32	0.32	0.73	0.88	0.61	0.74
1995	CGOA	8.0	0.50	0.38	0.87	0.95	0.79	0.91
1995	WYAK	8.0	0.63	0.55	0.90	0.94	0.88	0.94
1995	EYSE	8.0	0.55	0.75	0.84	na	0.83	na
1996	AI	8.0	0.06	0.11	0.84	0.91	0.64	0.76
1996	WGOA	8.0	0.35	0.25	0.81	0.88	0.69	0.74
1996	CGOA	8.0	0.66	0.37	0.93	0.93	0.90	0.82
1996	WYAK	8.0	0.64	0.32	0.94	0.98	0.94	0.90
1996	EYSE	8.0	0.55	0.50	0.88	0.95	0.87	0.92
1997	EBS	8.0	0.09	0.19	0.94	na	0.80	na
1997	WGOA	8.0	0.30	0.20	0.61	0.80	0.50	0.74
1997	CGOA	8.0	0.57	0.53	0.92	0.89	0.86	0.79
1997	WYAK	8.0	0.56	0.56	0.90	0.90	0.87	0.90
1997	EYSE	8.0	0.50	0.50	0.87	0.70	0.86	0.57
1998	AI	8.0	0.09	0.15	0.76	0.86	0.57	0.71
1998	WGOA	8.0	0.33	0.23	0.72	0.91	0.63	0.74
1998	CGOA	8.0	0.44	0.38	0.91	0.90	0.88	0.86
1998	WYAK	8.0	0.46	0.54	0.90	0.87	0.90	0.88
1998	EYSE	8.0	0.49	0.51	0.88	0.94	0.81	0.97
Average			0.43	0.39	0.85	0.89	0.78	0.82
Average paired difference				–0.04		0.05		0.04
Average paired ratio				1.04				

Note: AI, Aleutian Islands; EBS, eastern Bering Sea; WGOA, Western Gulf of Alaska; CGOA, Central Gulf of Alaska; WYAK, West Yakutat; EYSE, East Yakutat/Southeast. na, not available.

paired comparisons differ significantly between the open-access and IFQ fisheries (two-sample t test, df = 37, $p < 0.001$).

The increase in fishery catch rates relative to standard survey catch rates implies that the catching efficiency of the longline fleet improved with the transition from the open-access to the IFQ fishery. A measure of the catching efficiency is the ratio of the fishery and survey catch rates. We paired the fishery and survey catch rates by region and year and divided the fishery by the survey catch rate. These paired ratios showed that fishery catch rates averaged 47% of survey catch rates during the open-access fishery and

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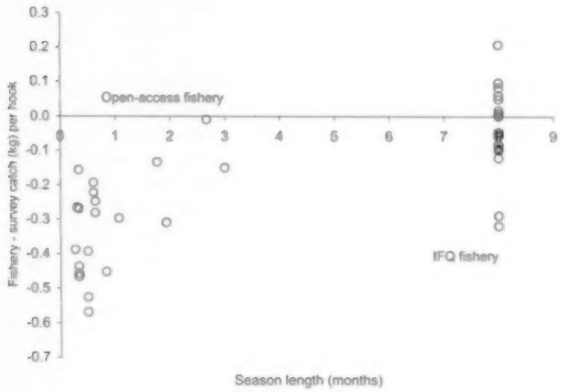
Fig. 1. Comparisons of longline fishery and longline survey catch per hook by region and year (1990–1998) versus season length. The regions are the North Pacific Fishery Management Council regions Bering Sea, Aleutian Islands, and the Gulf of Alaska regions Western, Central, West Yakutat, and East Yakutat/Southeast.



104% of the survey catch rates during the IFQ fishery. The change from 47% during the open-access fishery to 104% during the IFQ fishery implies that catching efficiency of the longline fleet increased 2.2 times with the transition from an open-access to an IFQ fishery.

Seasonal variation in catch rates probably inflated the estimate of how much catching efficiency improved. The open-access fishery and survey did not overlap; the fishery occurred during spring and the survey occurred during summer. We tested for seasonal variation in catch rates by examining IFQ fishery data for spring and summer from 1995 to 1998, years where seasonal data were available. We paired the spring and summer fishery catch rates by region and year and computed the paired differences. These paired differences showed that spring catch rates averaged 0.16 kg per hook less than summer catch rates, a significant difference (paired t test, df = 23, $p = 0.001$). A measure of the improved catching efficiency due to season is the ratio of the spring and summer catch rates. We paired the spring and summer catch rates by region and year and divided the spring by the summer catch rate. These paired ratios showed that spring catch rates averaged 82% of summer catch rates. Adjusting catching efficiency for the seasonal effect, estimated open-access fishery catch rates during summer averaged 57% of survey catch rates rather than 47%. Instead of increasing 2.2 times, the estimate of improved catching efficiency with the transition from an open-access to an IFQ fishery was 1.81 times.

The estimate of improved catching efficiency applies to the Gulf of Alaska but not to the Bering Sea and Aleutian Islands. The survey longline gear changed after 1994 for these two regions, so there are no control data from 1990 to 1998 to compare with the fishery data and estimate catching efficiency. Although no estimate is available, there is some evidence that catching efficiency did not change in the Bering Sea and Aleutian Islands. From 1994 to 1995, average fishery catch rate increased 111% in the Gulf of Alaska but only 9% in the Bering Sea and Aleutian Islands. The lack of a large increase for the Bering Sea and Aleutian Islands implies that catching efficiency remained the same, so for the rest of the paper, we assume that catching efficiency increased in the Gulf of Alaska but remained the same in the Bering Sea and Aleutian Islands.

Improved catching efficiency during IFQ management reduced the number of hooks and days at sea necessary to catch the quota. For example, in 1995, vessels deployed 50 million hooks during 4800 vessel-days (Table 5). Applying the relative efficiency of the IFQ and open-access fisheries, an open-access fishery would have required 80 million hooks and 7800 vessel-fishing days. Thus, the IFQ fishery required 3000 fewer days at sea to catch the quota. Fewer days at sea reduces variable costs such as fuel, bait, and gear. Cost data for Alaska groundfish fisheries are not available (Hiatt and Terry 1999); instead, we assumed that commercial fishery costs were the same as our longline survey costs. Fuel cost is based on 909 L per day and $\$0.264 \cdot L^{-1}$, bait cost is based on 5 kg of bait per 100 hooks and $\$0.88 \cdot kg^{-1}$, and gear cost is based on 39 000 hooks ($137 per thousand), 24 000 gangions ($95 per thousand for materials and labor), 11 500 beckets ($78 per thousand for materials and labor), and 40 boxes of groundline ($144 per box) required to replace worn gear during the annual longline survey, which deploys 546 400 hooks per year. The two longline vessel captains who reviewed our manuscript said that these values were reasonable estimates of fuel, bait, and gear costs for the commercial fishery. We estimated that commercial fishery costs for fuel, bait, and gear were $6 million for the 1995 IFQ fishery. An open-access fishery would have required $9.7 million. The landed value of sablefish in 1995 was $111 million, so IFQ management reduced these costs from 9 to 5% of landed value (Table 5). We also estimated the cost effect for the 1995–1998 fisheries. IFQ management reduced the total number of hooks fished by 38%, from 263 million to 164 million, or about 25 million hooks per year. Fuel, gear, and bait costs decreased from $33 million to $20 million, or about $3.1 million per year. Compared with landed value, these fuel, gear, and bait costs decreased from 8 to 5% of landed value.

Mature fraction

Fewer immature fish were captured with the transition from an open-access to an IFQ fishery. The difference was more obvious for females than for males. For females, fishery mature fraction by region and year averaged 0.65 during the open-access fishery and 0.82 during the IFQ fishery (during summer), an increase of 17 percentage points (Table 4). For males, fishery mature fraction by region and year averaged 0.78 during the open-access fishery and 0.89 during the IFQ fishery (during summer), an increase of 11 percentage points. Fishery mature fraction increased even though survey mature fraction increased only from 0.82 to 0.85 for males and was unchanged at 0.78 for females. We paired the fishery and survey mature fractions by sex, region, and year and computed the paired differences to control for the effect of demographic changes on the fishery mature fraction (Fig. 2). These paired differences showed that for females, fishery mature fraction averaged 13 percentage points less than survey mature fraction during the open-access fishery but was four percentage points more than survey mature fraction during the IFQ fishery, an improvement of 17 percentage points.

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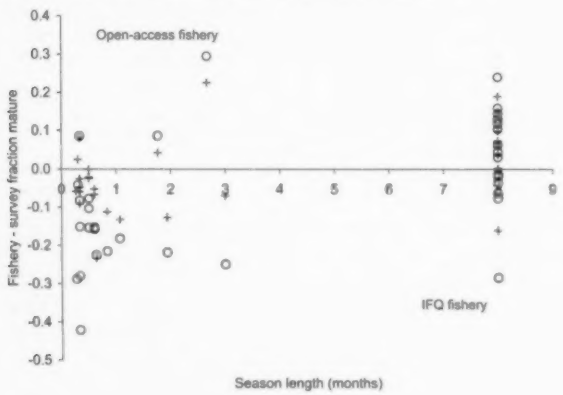
Table 5. Hooks, vessel-days, fuel, gear, and bait costs, their percentage of landed value, and landed value (Hiatt and Terry 1999) by year.

Year	No. of hooks deployed	No. of vessel-days	Fuel, gear, bait costs ($US)	% of landed value	Landed value ($US)
Open-access fishery					
1990	96 892 928	8844	11 424 585	13	86 000 000
1991	77 977 461	6991	9 133 668	9	97 900 000
1992	76 155 421	6931	8 969 807	10	91 900 000
1993	86 702 379	6013	9 310 659	10	97 400 000
1994	81 543 546	7170	9 483 863	8	114 400 000
Average				10	
IFQ fishery					
1995	49 681 040	4833	6 000 867	5	111 000 000
1996	44 691 335	4963	5 693 841	6	97 100 000
1997	34 356 229	3665	4 304 694	5	89 100 000
1998	35 025 506	3477	4 264 013	5	90 058 065
Average				5	
Assuming the catching efficiency of the open-access fishery					
1995	80 115 800	7793	9 677 017	9	
1996	72 395 174	8040	9 223 412	9	
1997	54 565 706	5820	6 836 858	8	
1998	56 231 048	5581	6 845 580	8	
Average				8	

Note: These values also are estimated for 1995–1998 assuming the reduced catching efficiency of the open-access fishery in the Gulf of Alaska.

Fig. 2. Comparisons of longline fishery and longline survey mature fraction by region and year (1990–1998) versus season length (months) for males (+) and females (○). The regions are the North Pacific Fishery Management Council regions Bering Sea, Aleutian Islands, and the Gulf of Alaska regions Western, Central, West Yakutat, and East Yakutat/Southeast.



For males, fishery mature fraction averaged four percentage points less than survey mature fraction during the open-access fishery but was five percentage points more than survey mature fraction during the IFQ fishery, an improvement of nine percentage points. These paired comparisons differ significantly between the open-access and IFQ fisheries for females (two-sample t test, df = 34, $p < 0.001$) and males (two-sample t test, df = 34, $p = 0.006$). The increase in fishery mature fraction relative to survey mature fraction implies that fishery selectivity of the longline fleet favored larger, older fish with the transition from the open-access to the IFQ fishery. The difference in mature fraction between the IFQ and open-access fisheries was not due to increased discards of small fish in the IFQ fishery because length sampling occurred before catch sorting and discarding.

Seasonal variation in mature fraction probably inflated the estimate of how much mature fraction increased with the transition from the open-access to the IFQ fishery. We tested for seasonal variation in mature fraction by examining fishery data for the spring and summer from years where seasonal data were available, 1995–1998. We paired the spring and summer fishery mature fractions by sex, region, and year and computed the paired differences. These paired differences showed that for both females and males, spring mature fraction averaged eight percentage points less than summer mature fraction. These paired comparisons differ significantly for males (paired t test, df = 17, $p = 0.003$) but not for females (paired t test, df = 18, $p = 0.086$). The increase in fishery mature fraction implies that larger, older fish are more available to the fishery in summer than in spring. We adjusted the mature fraction from the open-access fishery for the season effect by subtracting eight percentage points from the differences in mature fraction between the survey and open-access fishery. This adjustment reduces the improvement in mature fraction to nine percentage points for females and one percentage point for males.

The decreased harvest of immature fish in the IFQ fishery improves the chance that individual fish will reproduce at least once. We completed a spawning biomass per recruit analysis (Gabriel et al. 1989) to evaluate the effect of the reduced harvest of immature fish on the spawning potential of sablefish. A spawning biomass per recruit analysis evaluates the total contribution of a cohort to the spawning stock biomass over the cohort's lifetime, scaled by the original number of recruits, to provide a relative measure of spawning

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potential regardless of the absolute number of recruits. In our spawning biomass per recruit analysis, we assumed that the reduced harvest of immature fish in the IFQ fishery was due to differences in selectivity between the open-access and IFQ fisheries and that the growth, maturity at age, natural mortality, average recruitment, and average catch were the same. Selectivity refers to both selectivity of the longline gear and availability to the longline fishery. The age of 50% selection (the average age of first capture) was adjusted to match mature fraction estimated for the open-access and IFQ fisheries during summer. Values assumed for growth, maturity at age, natural mortality, slope of the selectivity function, average recruitment (13.7 million, the average value for the 1982–1995 year-classes), and average catch (17 000 t, the average value for 1995–1998) were obtained from age-structured modeling completed for the sablefish stock assessment (Sigler et al. 1999). The spawning biomass per recruit analysis showed that spawning potential was higher for the IFQ fishery compared with the open-access fishery. Spawning biomass per recruit was 9.2 kg per recruit for the open-access fishery and 10.0 kg per recruit for the IFQ fishery, a 9% increase.

Areas and depths fished

More areas were fished during the open-access fishery compared with the IFQ fishery. The upper continental slope was fished in all years regardless of fishery type, but during the open-access fishery, two major cross-shelf gullies additionally were fished (Fig. 3). Observed sets often were located in Shelikof Trough during the open-access fishery but rarely during the IFQ fishery. Observed sets often were located in Amatuli (Seward) Gully during the open-access fishery and much less commonly during the IFQ fishery, except for 1995 in the eastern half of Amatuli Gully. Fishing only the upper continental slope during the IFQ fishery implies that these grounds are preferred over the cross-shelf gullies and that fishermen used the cross-shelf gullies during the open-access fishery due to crowding on the preferred upper continental slope. Some fishermen have confirmed this change to us, reporting that they fished in the cross-shelf gullies during the open-access fishery because the preferred upper continental slope was crowded.

Most areas of the upper continental slope have been fished during both the open-access and IFQ fisheries (Fig. 3). Less fishing effort was observed in the eastern Gulf of Alaska during the open-access fishery due to lower observer coverage rather than less fishing in this area. Although some fishing effort occurs in most areas of the upper continental slope, the proportion of fishing effort near fishing ports increased during the IFQ fishery (Fig. 4).

The depths fished did not differ substantially between the open-access and IFQ fisheries. Most fish were caught between 400 and 800 m depth regardless of year, except in 1992 and 1998, when many fish were caught at about 100 m (Fig. 5).

Crowding on the fishing grounds

The distance between sets by a vessel is a measure of the crowding on the fishing grounds. We examined the distance to the nearest set during the same day and during the previous week. The frequency distributions of the minimum distances for sets during the same day were similar for the open-access and IFQ fisheries (Fig. 6). Most sets were 1–6 km apart. The highest proportion was 2 km apart, which implies that 2 km is the shortest preferred distance between sets. Sets during the previous week usually were closer during the open-access fishery. During the open-access fishery, an average of 47% of sets had another set by the same vessel within 2 km but only 31% during the IFQ fishery (two-sample t test, df = 41, $p < 0.001$) (Fig. 7).

Setting gear at or near the same spot not only reduces subsequent catch rate but also fish size. For sets by the same vessel within 2 km of another, the catch rate on the next day's set averaged 17% less (paired t test, df = 991, $p < 0.001$). The mean length on the next day's set averaged 1% less (paired t test, df = 303, $p = 0.02$).

Discussion

Benefits of IFQ management

Eliminating the race for fish by switching to IFQ management increased fishery catch rates and decreased harvest of immature fish in the Alaska sablefish longline fishery. Catching efficiency increased 1.8 times, reducing variable costs to catch the quota from 8 to 5% of landed value, and saving an average of $3.1 million annually. Decreased immature harvest for the IFQ fishery improved the chance that individual fish will spawn at least once. Spawning potential of sablefish, expressed as spawning biomass per recruit, increased 9%. Improved catching efficiency is an economic benefit by decreasing variable costs associated with fishing such as fuel and bait. Improved spawning potential is a biological conservation benefit by increasing the number of fish that have a chance to spawn at least once. Catch rate estimates from the halibut fishery in British Columbia also have increased with implementation of an IFQ program, although the amount of increase is uncertain because only two scientific surveys were available for comparison and high variation and bias in their estimates limited their significance (Sullivan and Rebert 1998). These benefits support fishermen's testimony that "IFQs provided the opportunity to utilize better fishing...methods, reducing bycatch of non-targeted species..." (NRC 1999). North Pacific Fishery Management Council analysts also anticipated "improved efficiency of harvesting operations" in the Alaska sablefish and halibut fisheries once IFQ management was implemented (Pautzke and Oliver 1997).

These benefits arose because the most productive habitat was less crowded during the IFQ fishery and so the fleet no longer had to fish less productive habitat. For example, the cross-shelf gullies of Shelikof Trough and Amatuli Gully often were fished during the open-access fishery but have been fished much less often during the IFQ fishery. Sablefish are less abundant in cross-shelf gullies. Survey catch rate for Shelikof Trough averaged 61% of that for the adjacent slope from 1990 to 1994 and 52% from 1995 to 1998. The survey catch rate for Amatuli Gully averaged 80% of that for the adjacent slope from 1995 to 1998; 1995 was the first year that these gullies were fully surveyed. Sablefish also are younger in cross-shelf gullies. In 1996, the earliest year for which age information is available from the cross-shelf gullies, average age was 5 years in Shelikof Trough, about half

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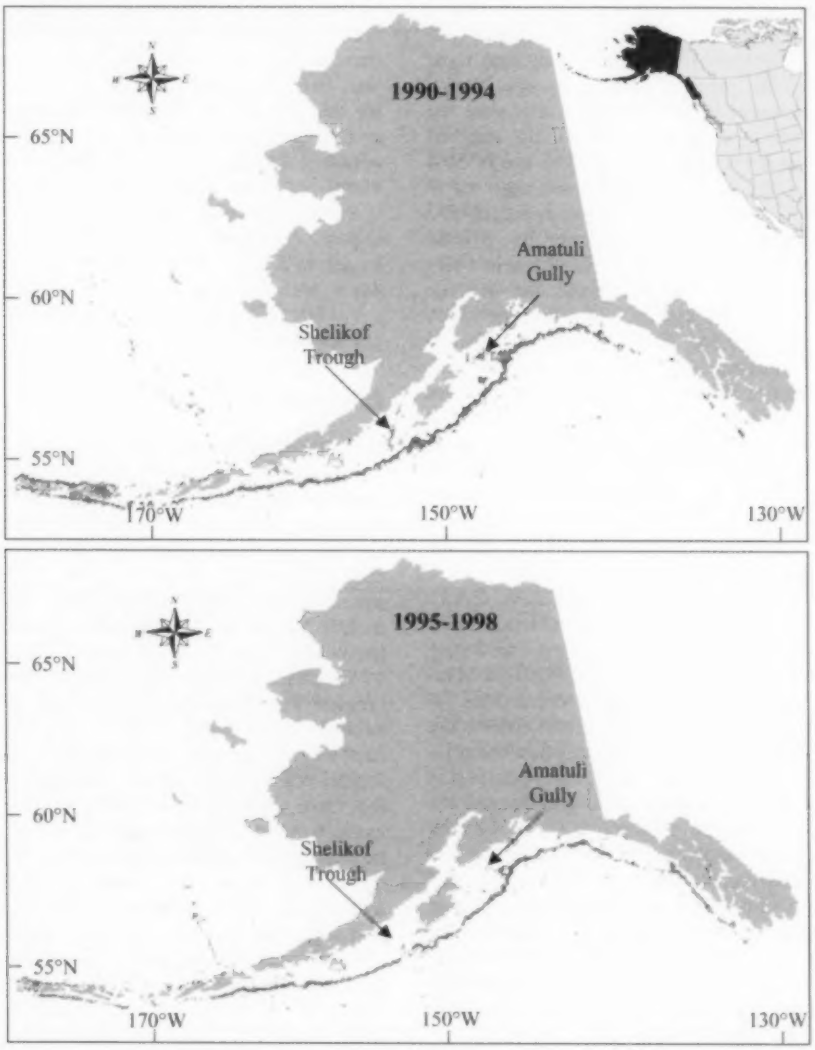
Fig. 3. Map of Alaska showing longline fishery set locations during the open-access fishery (1990–1994) and the IFQ fishery (1995–1998).



the age for the adjacent slope, and was 10 years in Amatuli Gully, about two thirds the age for the adjacent slope.

Less crowding on the fishing grounds with longer seasons also contributed to higher catch rates and larger fish landed. Sets on successive days by the same vessel generally were spaced closer together during the open-access fishery. By setting their gear at or near the same spot, the catch rate likely decreased due to local depletion. We found that for sets nearby one another (within 2 km), the catch rate on the next day's set averaged 17% less. Subsequent mean length was 1% less. Catch rate also decreased as the short seasons progressed in the open-access halibut fishery (Quinn 1987, table II). The rate of decrease was related to season length. The decrease ranged from 3% per day for a 20-day season to 15% per day for a 6-day season.

The sablefish fishing grounds were crowded during the open-access fishery because hundreds of vessels were fishing the limited area preferred by the fishery. The sablefish fishing grounds lie along the narrow upper continental slope of the Gulf of Alaska, Aleutian Islands, and eastern Bering Sea. The area fished during the 8-month-long IFQ fishery and presumed preferred by the fishery is about 43 000 km^2 in the Gulf of Alaska. In 1994, the last year of the open-access fishery, 1075 vessels landed sablefish in the Gulf of Alaska (Hiatt and Terry 1999), leaving about 40 km^2 per vessel. All vessels likely fished at the same time because the open-access season started on the same day, which implies a fishing area only 8 km (average set length in the directed fishery for sablefish in 1994) by 5 km for each vessel to fish during the open-access fishery.

Vessels naturally will crowd over good fishing grounds and near ports to reduce the costs of fishing. However, crowding on the grounds may prevent vessels from fishing these preferred areas. Crowding during the sablefish open-access fishery led to effort in less productive areas and farther from ports, but effort shifted to more productive areas

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Fig. 4. Proportion of effort by latitude for the East Yakutat/Southeast region for the open-access fishery (1990–1994) (◆) and the IFQ fishery (1995–1998) (+). An important fishing port, Sitka, Alaska, is located at 57°N. Latitude is rounded to the nearest 0.5°.

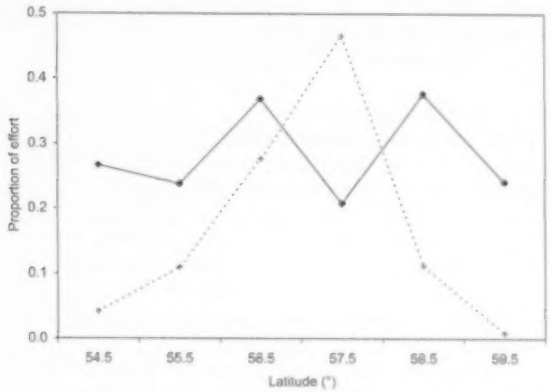
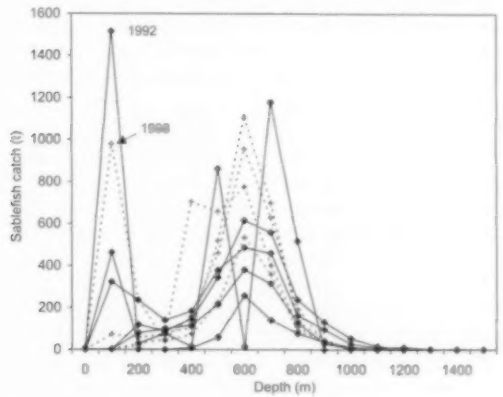


Fig. 5. Observed sablefish fishery catch versus depth by year for the open-access fishery (1990–1994) (◆) and the IFQ fishery (1995–1998) (+). Depth is rounded to the nearest 100 m.



and near ports during the longer IFQ seasons. Fleet effort in the British Columbia halibut fishery also shifted to areas of higher catch rate and closer to port with implementation of an IFQ program (Sullivan and Rebert 1998), although fishermen earlier reported little change in travel distance (Casey et al. 1995).

We expected a wider range of depths to have been fished during the open-access fishery compared with the IFQ fishery, anticipating that crowding on the fishing grounds would cause some fishing in less preferred depths. However, the depth range was not larger. The lack of a discernable difference may be due to the coarseness of the position and depth data. Position and depth were recorded at only one point, the start of gear retrieval, even though the gear typically stretches over several kilometres, and may not accurately represent the distribution of depths fished. We also expected, but did not find, that the distance between sets on the same day for the same vessel would be smaller during the open-access fishery compared with the IFQ fishery. However, the between-set distances calculated from the single recorded

Fig. 6. Frequency distributions of the distance to the nearest observed set on the same day by the same vessel for the open-access fishery (1990–1994) (◆) and the IFQ fishery (1995–1998) (+). Distance is rounded to the nearest kilometre.

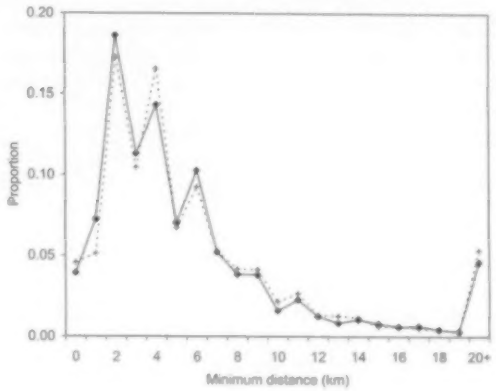
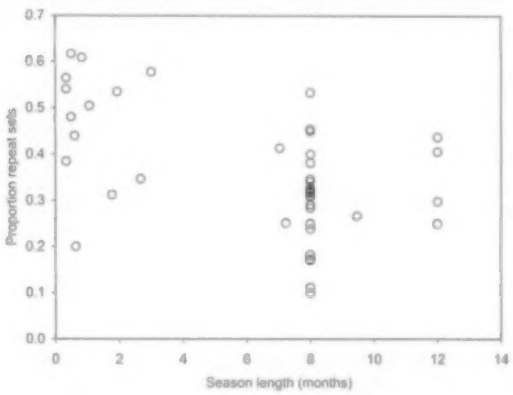


Fig. 7. For longline fishery sets by the same vessel and during the previous week, the proportion of sets by region and year where the minimum distance to the nearest set was less than or equal to 2 km ("repeat" set) versus season length. The regions are the North Pacific Fishery Management Council regions Bering Sea, Aleutian Islands, and the Gulf of Alaska regions Western, Central, West Yakutat, and East Yakutat/Southeast.



points may not accurately represent the distribution of between-set distances. Position also was recorded only to the nearest minute of latitude and longitude, corresponding to an accuracy of about 2 km north–south and 1 km east–west at the latitude of the Alaska sablefish fishery. The position data may be too coarse to discern small differences in between-set distances. In addition, there likely is an optimum between-set distance, regardless of crowding, that minimizes travel time between sets and places sets far enough apart so as not to compete with one another.

Trip limits and fishery cooperatives

The benefits of the IFQ fishery probably accrued because of the lengthened season, which slowed the pace of the fishery. The catch occurs over several months and the vessels no longer are forced to fish side by side. An alternative manage-

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ment method that also lengthens the season is trip limits. A trip limit is a catch ceiling for an individual fishing trip. Unlike IFQs, trip limits do not require setting annual catch quotas. A trip limit can achieve some of the objectives possible with IFQs but also can have major detrimental impacts. A trip limit extends the supply of fish to processing plants and the consumer through a greater part of the year like an IFQ fishery. However, discarding of fish occurs when catches exceed the trip limit (Pikitch et al. 1988; Richards 1994), species may be misreported (Richards 1994), and discarding and misreporting lead to underestimates of both catch and catch rate (Richards 1994). Sablefish discards were larger for trip limit management off Oregon, 15–20% (Pikitch et al. 1988), than for IFQ management off Alaska, 2–5% (Hiatt and Terry 1999). Discarding of sablefish also may occur in the IFQ fishery when the IFQ is reached but occurs once per year rather than for every trip. Vessels averaged four IFQ sablefish trips per year during 1997 and 1998. Size-selective discarding may occur for each trip and is discussed in the "Selective fishing practices" section.

Fishery cooperatives that divide the quota into quasi-IFQs now operate in the west coast whiting and Bering Sea pollock fisheries, beginning in 1997 and 1999, respectively. Benefits associated with eliminating the race for fish also may occur for fishery cooperatives. Anticipated benefits of the whiting cooperative include more efficient allocation of resources by fishing companies, improvements in processing efficiency and product quality, and a reduction in waste and bycatch rates relative to the former "derby" fishery in which all vessels competed for a fleet-wide quota (Dorn et al. 1999). These cooperatives reportedly have slowed the pace of the fisheries, reduced overcapitalization (fewer boats chasing the fish in the pollock fishery (Anonymous 2000)), increased product recovery, and, in the case of the Bering Sea pollock fishery, made it easier for the fleet to respond to the required and prudent alternatives for protection of the Steller sea lion, which is endangered in western Alaska (North Pacific Fishery Management Council 1999).

Estimated value of increased catching efficiency

IFQ management improved catching efficiency compared with open-access management, thereby reducing the number of hooks and days at sea necessary to catch the fish. IFQ management reduced fuel, gear, and bait costs from 8 to 5% of landed value, or about $3.1 million per year, compared with open-access management. The reduction in number of hooks was 38% or about 25 million hooks per year. The race for fish during the open-access fishery clearly decreased overall benefits from the fishery. Arnason (1996) cited the five- to sixfold increase in value of the quota shares in the Icelandic demersal fisheries as evidence for improved efficiency. He hypothesized that the increased value was due to reduced capitalization and fishing effort. Our study of the sablefish IFQ fishery supports his hypothesis. We found that the slower pace of the IFQ fishery led to increased fishery efficiency and reduced fishing effort.

At the time of the North Pacific Fishery Management Council deliberations on the sablefish and halibut IFQ program, analysts estimated that the total annual benefits of the IFQ program for both sablefish and halibut would range from $30.1 to $67.6 million (Pautzke and Oliver 1997). Among these anticipated benefits were reductions in harvesting costs by $12.4 million to $13.6 million because of increased flexibility in selecting fishing strategies and the redistribution of catch and effort to lower the cost of fishing operations. The $3.1 million reduction in annual costs that we estimated for the sablefish fishery shows that at least one of these anticipated benefits of IFQs, to "improve efficiency of harvesting operations," has been achieved.

Selective fishing practices

Reducing the number of hooks required to land the catch likely also reduced habitat effects of fishing longline gear. Invertebrates such as coral, anemones, and sea stars commonly are snagged and brought to the surface with longline gear; however, documentation of how longline affects the seafloor and associated species is limited and these effects have not been quantified. High (1998) and K.J. Krieger (National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratory, Juneau, Alaska, unpublished data) incidentally reported underwater observations of longline. High (1998) observed coral snagged by longline; he noted that unless lifted off bottom, sturdy flexible corals appeared to be relatively unharmed by the longline, whereas more fragile hard corals often had portions broken off. Krieger observed small *Primnoa* colonies attached to <0.4-m-diameter boulders that had been tipped and dragged, which he attributed to longline gear. Although the effects of longline gear are poorly known, to whatever unknown extent the habitat is affected, the reduced number of hooks deployed during the IFQ fishery reduces these habitat effects. This serendipitous effect fulfills a requirement of the Sustainable Fisheries Act of 1996, an amendment of the Magnuson–Stevens Fishery Conservation and Management Act, for fishery management councils to employ conservation and enhancement measures that minimize impacts and protect and restore that habitat.

The IFQ fishery is preferable to the open-access fishery in terms of spawning biomass per recruit; spawning potential is 9% greater for the IFQ fishery compared with the open-access fishery. Fewer immature fish were captured with the transition from an open-access to an IFQ fishery. The decreased harvest of immature fish improves the chance that individual fish will reproduce at least once.

The increased mature fraction of the catch during the IFQ fishery is not due to discards because the observer collects length information before any size sorting of the catch. Although discards did not affect our analysis, discards may occur in the IFQ fishery. During the open-access fishery, there was no motivation to discard small fish because of the short duration of the fishery and the subsequent desire to maximize catch and value. During the IFQ fishery, there is motivation to discard small fish because the value usually increases with fish size and each quota holder's catch is fixed. However, a harvester has to catch more fish to make up for highgrading, generating more operating expenses and foregoing the revenue associated with the small fish; for the sablefish IFQ fishery, highgrading is unlikely to be profitable (NRC 1999). Fisheries in which highgrading is not a serious concern seem to be characterized by minimal price differentials among fish sizes (Squires et al. 1995) and (or) relatively high costs of catching replacement fish (NRC 1999). The

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price differential for small sablefish is minimal, no more than 12.5% in 2000 (K. Hogan, The Auction Block, Homer, Alaska). A conservation concern also may motivate some fishermen to release small sablefish, which usually survive hooking if carefully released. There is a minimum size limit for halibut but not for sablefish. It may seem inconsistent to some fishermen to return viable, small halibut to the sea but not viable, small sablefish.

IFQ implementation

Implementing IFQs is controversial mainly because of socioeconomic concerns: the fairness of the initial allocations, the fairness of essentially privatizing harvest rights to a public resource, and the potential for consolidation of the fishery. In the United States, these and other issues have led to a moratorium on implementing new IFQ programs. On the other hand, IFQs eliminate the race for fish and the associated waste and danger of the short seasons. Our purpose was to examine how IFQ management affected catching efficiency and spawning potential in the Alaska sablefish fishery rather than to conduct an overall evaluation of sablefish IFQ management. We found that switching to IFQ management provided two clear benefits, increased fishery catch rates and decreased harvest of immature fish. These improvements occurred because less fishing takes place in marginal areas and localized depletion due to crowding of the fishing grounds is reduced. These two benefits should be weighed when considering other fisheries for IFQ management.

Acknowledgments

We thank Mary Furuness (National Marine Fisheries Service Alaska Regional Office) for tracking down historical season lengths for the Bering Sea and Aleutian Islands regions, Dean Adams (F/V *Quest*), Bill Clark (International Pacific Halibut Commission), Arne Fuglvog (F/V *Kamilar*), Chris Oliver (North Pacific Fishery Management Council), Alex Wertheimer (National Marine Fisheries Service Auke Bay Laboratory), and two anonymous reviewers for reviewing this paper.

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Niche breadth in clonal and sexual fish (*Poeciliopsis*): a test of the frozen niche variation model

Melissa M. Gray and Stephen C. Weeks

Abstract: The evolution and subsequent maintenance of sex has been debated for many years, and there are numerous aspects that remain poorly understood. When comparing sexual with asexual reproduction, there are many more apparent benefits to being asexual than sexual. The frozen niche variation (FNV) model describes how asexual clones can arise from a sexual population and how the two reproductive types can coexist. Herein we compared three sympatric populations of sexual and asexual fish (one sexual population, *Poeciliopsis monacha*, and two clonal populations, *P. 2-monacha-lucida*) to test the assumption of the FNV model that sexual populations have a broader dietary niche (as measured by gut contents analysis) than clonal populations. Individual sexual fish had similar dietary breadth when compared with clonal individuals. However, dietary breadth for sexual populations as a whole was broader than for either clonal population, indicating differences in between-individual dietary choice. Our results support the primary assumption of the FNV model and thereby provide a possible explanation for the maintenance of sexual reproduction in this clonal–sexual complex.

Résumé : L'origine et le maintien de la sexualité font l'objet de débats depuis de nombreuses années et il y a plusieurs aspects de la question qui sont encore mal compris. Il semble y avoir beaucoup plus d'avantages à la reproduction asexuée qu'à la reproduction sexuée. L'hypothèse du gel de la variation de la niche (FNV, « Frozen Niche Variation ») illustre comment des clones asexués peuvent surgir de populations sexuées et comment les deux types de reproduction peuvent coexister. On trouvera ici une comparaison de trois populations sympatriques de poissons sexués et asexués (une population sexuée, *Poeciliopsis monacha*, et deux populations clonales, *P. 2-monacha-lucida*) qui vise à vérifier les présuppositions du modèle FNV selon lesquelles la niche alimentaire des populations sexuées (mesurée par l'analyse du contenu du tube digestif) est plus étendue que celle des populations clonales. Les individus sexués ont une étendue de niche alimentaire semblable à celle des individus clonaux. Cependant, l'étendue de la niche de la population sexuée considérée dans son ensemble est plus grande que celles de l'une ou de l'autre des populations clonales, ce qui indique qu'il y a des différences de choix alimentaires entre les individus. Nos résultats sont en accord avec la présupposition fondamentale du modèle FNV et ils fournissent donc une explication possible au maintien de la reproduction sexuée dans ce complexe sexué–clonal.

[Traduit par la Rédaction]

Introduction

The evolution of sex has intrigued scientists for many years, stimulating the generation of numerous arguments and theories about the origin and maintenance of sex (Williams 1975; Bell 1982; Kondrashov 1993). Asexually reproducing individuals require less energy, time, and resources than sexually reproducing individuals and can thus produce twice the number of offspring (Williams 1975). However, sexual reproduction is still commonplace despite these apparently overwhelming advantages to asexual reproduction (Bell 1982).

There is an array of theories about the benefits to sex (Kondrashov 1993) but only two have gained widespread acceptance: the mutation accumulation hypothesis, wherein an asexual lineage slowly "melts down" because of its inability to purge deleterious mutations (Muller 1964; Kondrashov 1988; Lynch and Gabriel 1990), and the Red Queen hypothesis, wherein sexuality is advantageous for avoidance of rapidly evolving parasites and viruses (Bell 1982; Hamilton et al. 1990). Of the two, the Red Queen hypothesis has had the greatest empirical support (Dybdahl and Lively 1995; Jokela et al. 1997; Johnson 2000).

Although the Red Queen hypothesis has generally broad acceptance, one well-studied unisexual–sexual species complex, the topminnow *Poeciliopsis*, is not well explained by this model (Weeks 1996) but remains best explained by a third hypothesis: the frozen niche variation (FNV) model (Vrijenhoek 1979, 1984, 1994). In this model, sexuals are assumed to have a wider niche breadth than the clones, which should then translate to lower inter-individual competition among sexuals compared with that among clones (Bell

Received December 13, 2000. Accepted March 31, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 4, 2001.
J16132

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 DOI: 10.1139/cjfas-58-7-1313 © 2001 NRC Canada

1982; Case and Taper 1986; Weeks 1993). Assuming such a difference in relative niche breadth, a sexual population can avoid replacement by a few clones by being able to use resources unavailable to the clones. In this model, genotypes are assumed to be "frozen" into clones by hybridization events between two closely related sexual species (Vrijenhoek 1979, 1984) or by random mutations within a single sexual population (Weeks 1993). Over time, there is assumed to be a constant extinction and rebirth of different clonal populations, and consequently, the clones are assumed to arise from polyphyletic origins (Vrijenhoek 1979, 1984). If the creation of viable clones is low enough, the random extinction of these clones is great enough, and the sexuals' niche is sufficiently broader than that of the clones, then the sexual populations can resist replacement even though they incur the twofold cost of sex (Weeks 1993). In many respects, the FNV model is similar to the Tangled Bank model, as outlined in Bell (1982; see also Case and Taper 1986).

Many of the assumptions and predictions of the FNV model have been successfully tested and confirmed (Vrijenhoek 1994). The recurrent production of clones has abundant empirical support in natural asexual populations (Uzzell 1964; Dybdahl and Lively 1995; Johnson and Bragg 1999). The assumption that the sexual ancestor(s) have considerable genetic variability for ecologically relevant traits, thereby allowing the freezing of ecologically distinct clones, has been thoroughly addressed using clonal and sexual populations of *Poeciliopsis*. Wetherington et al. (1989) found considerable among-individual genetic variation for size at birth, juvenile growth, and early reproduction among "hemiclones" that were artificially produced from two *Poeciliopsis monacha* populations. Schenck and Vrijenhoek (1986, 1989) found both spatial and dietary differences among sexual and clonal populations of two unisexual biotypes of *Poeciliopsis* in their native streams. Weeks et al. (1992) described differences in feeding behavior between two naturally co-occurring hemiclones and their sexual progenitors, which corresponded with natural differences in diets in field-caught fish.

The prediction that genotypic differences in ecologically relevant traits leads to niche partitioning in clonal and sexual populations has had mixed support. Vrijenhoek (1979) has shown that sexuals constitute a smaller proportion of *Poeciliopsis* populations in streams where clonal diversity is high relative to monoclonal streams, which is consistent with the notion that the clones are usurping a higher proportion of the "niche space" in populations where their combined resource breadth is largest. Semlitsch et al. (1997) found that mixed clonal populations performed better than single clonal populations of the hybridogenetic frog *Rana esculenta* in artificial ponds. However, Weeks (1995) found no evidence of niche partitioning in clonal and sexual populations of *Poeciliopsis* raised under high-density treatments in the laboratory. One possible explanation for this lack of partitioning is that the laboratory environment was not heterogeneous enough to allow significant niche partitioning (Weeks 1995). Nonetheless, the combined evidence suggests that genetically determined, ecologically relevant phenotypic differences among clonal lineages and between clones and sexuals are likely to facilitate coexistence between clonal and sexual populations, as predicted by the FNV model.

One of the critical assumptions of the FNV model is that sexuals should have a broader niche than a single clone (Vrijenhoek 1979, 1984, 1994). To date, this assumption has not been directly tested in the *Poeciliopsis* species complex (Vrijenhoek 1994). Herein we report the results of a dietary study of sexual and clonal *Poeciliopsis* collected from natural populations. We partition total dietary breadth into within- and between-individual components to test the assumption that sexual *Poeciliopsis* have a greater between-individual dietary breadth than coexisting clones.

Materials and methods

Fish strains and collection locations

Three *Poeciliopsis* (Atheriniformes: Poeciliidae) strains were analyzed in this experiment: an outcrossed sexual strain (*P. monacha* Miller) and two associated unisexual, triploid strains (*P. 2-monacha-lucida* MML/I and MML/II, hereafter referred to as Clone 1 and Clone 2, respectively; Vrijenhoek et al. 1977). The triploid *Poeciliopsis* reproduce gynogenetically, a strictly clonal mode of reproduction whereby the entire triploid genome is faithfully replicated among generations (Schultz 1969). Although sperm from a sexual species is required to activate embryogenesis in the triploid ova, paternal genes make no contribution to the genotype of the offspring (Schultz 1967; Cimino 1972; Vrijenhoek 1972). For further information on this reproductive complex, see Schultz (1969).

A total of 427 fish (80 Clone 1, 33 Clone 2, and 314 *P. monacha*) were collected from pools in the Arroyo de los Platanos region of the Rio Fuerte, Sonora, Mexico (26°30′N, 108°30′W; see Moore and Eisenbrey (1979) for further details of the region), during May 1990. During this time of year, the stream dries into small, isolated pools that are either completely isolated or are interconnected by only small rivulets of water. This isolation results in a number of pools that are essentially "closed systems," with only a slight amount of migration among pools (Moore and Eisenbrey 1979). Nine of the most isolated of these pools were chosen to maximize the likelihood that the fish measured from each pool were likely experiencing conditions in that pool rather than being migrants from nearby pools. The pools were aligned in a linear array, with Pool 1 at the head of the stream and Pool 9 about 1 km downstream. The intervening pools were scattered along this length, with at most several hundred metres separating one pool from the next (Weeks 1996). The number of fish of each strain collected at each pool was as follows: Pool 1, 18 Clone 1 and 32 *P. monacha*; Pool 2, 8 Clone 1 and 40 *P. monacha*; Pool 3, 12 Clone 1, 7 Clone 2, and 16 *P. monacha*; Pool 4, 10 Clone 1 and 40 *P. monacha*; Pool 5, 10 Clone 1, 8 Clone 2, and 32 *P. monacha*; Pool 6, 1 Clone 1 and 48 *P. monacha*; Pool 7, 4 Clone 1 and 40 *P. monacha*; Pool 8, 8 Clone 1 and 42 *P. monacha*; Pool 9, 9 Clone 1, 18 Clone 2, and 24 *P. monacha*. Because we wished to compare only pools with coexisting strains, we removed Pool 6 from the analyses, thus allowing a total of 378 fish (79 Clone 1, 33 Clone 2, and 266 *P. monacha*) to be analyzed in this study.

The fish analyzed in this comparison were previously used to compare clonal and sexual strains differing in external parasitism (Weeks 1996). In that experiment, the ovaries were removed for a comparison of reproductive health among parasitized and non-parasitized fish. In that project, care was taken to keep the intestinal tract intact. These fish were then stored individually in vials with 70% ethanol until the recent examinations were conducted on their intact intestinal tracts. Sexual type and clonal identity were determined in a previous study (Weeks 1996) via starch–gel electrophoresis of muscle tissue.

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Table 1. Percentage of dietary items averaged across individuals and pools.

Dietary item	Clone 1	Clone 2	*P. monacha*
Algae	4.5	6.4	9.4
Other plants	3.4	1.7	4.6
Detritus	78.4	72.5	72.3
Nematodes	2.2	3.9	0.2
Trichopterans	1.4	1.4	2.5
Ephemeropteras	2.7	7.1	3.4
Chironomids	1.8	2.4	1.8
Other invertebrates	2.8	0.9	2.4
Adult fish scales	0.0	0.0	0.6
Whole *Poeciliopsis* juveniles	1.8	1.8	1.1
Terrestrial invertebrates	0.8	1.8	0.8
Aquatic invertebrates	0.3	0.2	0.9

Analysis of gut contents

Dietary analyses were conducted on females only (see Weeks 1996). A dissecting scope (Olympus SZH (Olympus of America, Inc., Mellville, N.Y.)) equipped with an ocular micrometer was used to examine the intestinal tracts of these fish. When the appropriate magnification was determined, the micrometer scale was calibrated to a metric scale. The length of the whole intestinal tract was measured and recorded and then was partitioned into sections of 100 µm. If the ending section was less than 50 µm, it was left attached to the previous 100-µm section. If the ending section was greater than 50 µm, it was analyzed as a separate section. All sections were opened and the contents were examined. The items found were then placed into one of 12 categories and given a proportion based on the volume of the intestinal tract occupied by that item in that 100 µm section of the intestinal tract. When all sections were examined, a weighted total proportion was computed for each dietary item. Thus, data consisted of the categories of food items consumed and their relative proportion (p) in the diet of each fish.

Statistical analyses

Within- and between-individual dietary breadth was estimated following the procedures outlined in Case (1990). The within-individual measures (B) were calculated using the Simpson Index (Simpson 1949). This measure was calculated for each fish within each strain and in each of the nine pools and is simply the inverse of the sum of the squared proportions (p) of all items consumed by an individual (i.e., $[\Sigma p_i^2]^{-1}$, where $i = 1$ to x and x = total number of food items consumed; Case 1990). Natural log-transformed B values were normally distributed and thus were analyzed using parametric methods. B values were analyzed in a blocked one-way analysis of variance, using pools as the block and fish strains as the main effect (SAS 1985).

The between-individual dietary overlap values (α) were calculated using the proportion of the diet of a particular food item consumed by two fish of the strain in question, adjusted for the within-individual dietary breadth, B (Case 1990). Each individual fish within a strain was compared with all others in that strain using the following overlap calculation:

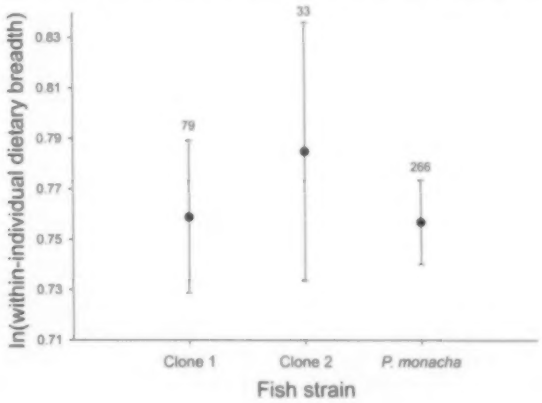
$$(1) \qquad \alpha_{l,j,k} = B_{j,k} \Sigma p_{i,j,k} p_{i,l,k}$$

The above calculation measures the dietary overlap of individual l with individual j in fish strain k by comparing the sum of the products of all i food items consumed (Case 1990). For example, in a population of 10 individuals, there would be 9 α's calculated per individual, for a total of 90 α's in the sampled population. Given this multiple set of calculations per individual, the α's are not conducive to parametric analyses (see Case 1990). Therefore, the overlap values generated using Case's procedure were compared using 95% confidence intervals generated using a bootstrapping procedure to produce a distribution of estimates for each fish strain (1000 runs; see Dixon 1993). Between-individual overlaps were constructed both within pools (for Clone 1 and *P. monacha*) and for all strains grouped across pools.

Table 2. ANOVA of the natural log of within-individual dietary breadth (B) for all three fish strains.

Source	df	Sum of squares	F ratio	P value
Pools	7	7.271	14.773	0.0001
Fish strain	2	0.013	0.093	0.9112
Error	368	25.876		

Fig. 1. Within-individual dietary breadth (B) for the three fish strains averaged across pools. Error bars indicate two standard errors of the mean. Numbers above error bars are sample sizes.



Results

Dietary items consumed by the three fish strains were grouped into the following categories for dietary comparisons: aquatic algae (Algae), other plant material (Plants), nematodes, Trichopteran larva, Ephemeropteran larve, Chironomid larva, *Poeciliopsis* spp. juveniles, terrestrial invertebrates (spiders, mites, grasshoppers, Odonata, Diptera, Coleoptera), fish scales (from *Poeciliopsis* adults), aquatic invertebrates (Isopods, Copepods, Amphipods, snails), other invertebrates (any unidentified invertebrates), and detritus (unidentified organic matter). In all three fish strains, detritus was the most abundant food item found in the intestinal tracts (Table 1). Plant material (especially algae) and aquatic insects were the next most abundant food items. All other food items were generally uncommon (<5% of diet).

The within-individual dietary breadth did not differ among any of the three fish strains (Table 2, Fig. 1), indicating that all three strains had similarly diverse diets within an individual (i.e., all were similar on a specialist to generalist scale). There were significant pool-to-pool differences in diet, with fish in some pools having much more diverse diets than those in other pools. A comparison of within-individual dietary breadth of only Clone 1 and *P. monacha* revealed that

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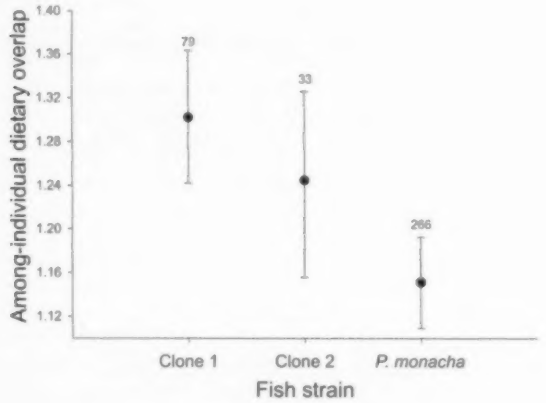
Fig. 2. Between-individual dietary overlap for the three fish strains averaged across pools. Error bars indicate the 95% confidence interval of each mean (calculated by bootstrapping; see text for further information). Numbers above error bars are sample sizes.



the interaction of pools and fish strain was not significant ($F_{7,329} = 0.424$; $P > 0.85$), suggesting that although diets differed among pools, the lack of a difference in within-individual dietary breadth between Clone 1 and the sexual strain was consistent across pools. Such a test could not be conducted for all three strains as Clone 2 was found in only a subset of all nine pools.

Comparisons of between-individual dietary overlap revealed a much different pattern (Fig. 2). The sexual strain (*P. monacha*) had a significantly lower between-individual dietary overlap compared with Clone 1 when averaged across pools (Fig. 2). *Poeciliopsis monacha* also had lower overlap (but not significantly so) compared with Clone 2 across pools. Although Clone 2 was lower than Clone 1 in between-individual overlap, their 95% confidence intervals overlapped widely (Fig. 2), suggesting that this difference was not significant.

A comparison of the between-individual dietary overlap data for Clone 1 and *P. monacha* within pools showed the same trend, with *P. monacha* having lower dietary overlap than Clone 1 in five of eight pools examined. Only three of these eight comparisons revealed significant differences among strains, with all three showing lower between-individual dietary overlap for *P. monacha* than for Clone 1 (Table 3).

Table 3. Average between-individual dietary overlap for coexisting clones and sexuals by pool.

Pool	Clone 1	*P. monacha*
1	1.42 (1.32, 1.51)	**1.51** (1.42, 1.57)
2*	**1.37** (1.28, 1.47)	1.08 (0.91, 1.23)
3	**1.45** (1.31, 1.59)	1.41 (1.32, 1.49)
4	1.16 (1.01, 1.30)	**1.20** (1.11, 1.29)
5	**1.33** (1.08, 1.51)	1.23 (1.12, 1.31)
7*	**1.33** (1.28, 1.38)	1.24 (1.19, 1.28)
8*	**1.40** (1.30, 1.51)	1.01 (0.91, 1.10)
9	1.01 (0.84, 1.19)	**1.04** (0.85, 1.18)
Average	**1.30** (1.24, 1.36)	1.17 (1.13, 1.21)

Note: 95% confidence intervals are shown in parentheses. Larger values between strains are in bold. Pools in which the two strains differ significantly (at $P < 0.05$) are indicated by asterisks (*).

Discussion

The coexistence of a limited number of clones and sexuals can occur if the sexuals have a broader niche breadth relative to the combined niche breadth of the clonal population (Vrijenhoek 1984; Bell 1982; Case and Taper 1986). For this to be true generally, individual clonal strains must have a narrower niche breadth than coexisting sexuals (Case 1990). In cases where clones are continually frozen from the sexual population (Vrijenhoek 1979), clonal extinction is required in addition to the broader niche breadth for the sexuals to persist (Weeks 1993). Clonal and sexual fish in the genus *Poeciliopsis* have been thoroughly studied in attempts to understand what conditions promote coexistence (reviewed in Vrijenhoek 1994). However, to date, no study has directly compared relative dietary breadth between sexual and clonal types in this clonal–sexual species complex.

The results obtained herein support the assumption that sexual *Poeciliopsis* have a broader dietary breadth than do two coexisting clones. The dietary items consumed were similar to those reported in previous studies (Schenck and Vrijenhoek 1989; Weeks et al. 1992) in that detritus, algae, and aquatic insects were the major component of the diet of all three fish strains. One major difference is that a number of whole juvenile *Poeciliopsis* were found in the diets of all three strains in the current study, whereas only adult fish scales were found in previous field-collected specimens (Schenck and Vrijenhoek 1989). Cannibalism has been previously reported in the laboratory for these fish strains (Weeks and Gaggiotti 1993; R.C. Vrijenhoek, Monterey Bay Aquarium Research Institute, 7700 Sandholt Road, Moss Landing, CA 95039-9644, personal communication), but this is the first documented example of cannibalism from their native habitat. Overall, we found equivalent levels of within-individual dietary breadth when we compared diets among strains, indicating that all three fish strains were similar in their level of within-individual dietary generalization.

Conversely, when we compared between-individual dietary overlap, the sexuals were found to have less dietary overlap than the clones, indicating that each clonal strain consumed a less diverse range of food than the sexuals. The combined within- and between-individual comparisons imply that although the sexual individuals are not dietary generalists, they each choose to eat slightly different food items. Thus, the combined diets of all sexuals lead to a more diverse diet as a population than observed within the two clonal populations. If such dietary choices are partially genetically determined, then they suggest that the genetic diversity of the sexual population translates into a wider array of food items consumed by the sexuals than by either clone. This greater dietary breadth in the between-individual dietary component but no difference in the within-individual dietary component is exactly the pattern assumed by the FNV model (Vrijenhoek 1979, 1984). If sexuals were to have a greater overall dietary breadth merely because of being greater individual food generalists, competition among sexuals would

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be similar to that among clones. If this occurred, then the reproductive advantage of the clones would drive the sexuals to extinction (Vrijenhoek 1979, 1984). These findings thus provide strong confirmatory evidence that the niche-partitioning predicted by the FNV model can provide the necessary conditions allowing clonal and sexual coexistence in this species complex.

Additional, although only circumstantial, evidence suggests that genotypic diversity translating to dietary breadth can be found by comparing the niche breadths of Clones 1 and 2. Moore and Eisenbrey (1979) found that Clone 2 is made up of four minor subtypes (identified by tissue grafting), whereas Clone 1 is truly a single clone. If these grafting subtypes also differ in dietary or behavioral characters, then they might be expected to have a wider between-individual niche breadth than any single clone. It is interesting to note that Clone 2 has an intermediate between-individual dietary overlap relative to Clone 1 and *P. monacha*. Because differences in dietary overlap between Clones 1 and 2 were not significant, we cannot assert that the more genetically diverse Clone 2 indeed has a broader diet than Clone 1. Nevertheless, the relative ranks of the three fish strains is exactly that assumed by the FNV model (Vrijenhoek 1979, 1984), with the monoclonal population having the narrowest diet, followed by the polyclonal population (Clone 2), with the sexual population having the broadest diet.

The only other system so far studied for dietary breadth is the clonal–sexual lizard *Cnemidophorous*. Case (1990) did a detailed dietary comparison of clonal and sexual *Cnemidophorous* in Arizona and found the same pattern as we describe here: clonal lizards had a narrower between-individual dietary overlap compared with coexisting sexual lizards, whereas there was no difference in dietary breadth found within-individuals (i.e., individual sexuals were not greater generalists than the clones). Case (1990) also interpreted this as evidence that the between-individual dietary breadth was due to genetically determined dietary differences among sexuals, as assumed in the FNV model (Vrijenhoek 1979, 1984). In a separate study, Paulissen et al. (1988) found that polyclonal populations of *Cnemidophorus* had increased dietary breadth relative to monoclonal populations, although they did not partition dietary breadth into within- and between-individual components. Therefore, the current results on *Poeciliopsis* are consistent with the only other tests of relative dietary breadth in clonal–sexual hybrid vertebrates.

Some of the dietary differences documented in this study might be partially due to behavioral differences. Schenck and Vrijenhoek (1986, 1989) found that Clones 1 and 2 tended to frequent areas where there was current and that the sexuals prefered still waters. This spatial niche partitioning could cause some of the variation in dietary choice found in the present study. Different aquatic and terrestrial insect prey may occur in these different parts of the pool because of current and air movement.

A comparison of between-individual dietary overlap of Clone 1 and the sexual fish of each pond was made to see how overlaps values compared from pool to pool. We found that three of eight ponds showed significant differences in between-individual dietary overlap, with the sexual fish having less overlap than Clone 1 fish. Two additional ponds showed trends in that direction. Thus, the greater dietary diversity for the sexuals is not merely due to combining fish caught in different pools (which may have different prey items) but is a true reflection of a wider dietary breadth both within and among pools.

The FNV model asserts that sexual reproduction is advantageous in heterogeneous environments because individuals have slightly different ecological requirements (Vrijenhoek 1979, 1984). Each clonal population has its own, narrow requirements, thereby allowing sexuals and clones to coexist (see also Bell 1982; Case and Taper 1986). This study reports evidence in favor of the FNV model: sexuals have a wider niche breadth than either coexisting clone in a naturally heterogeneous environment. Such a reduced niche overlap should mean less competition between individuals for food, which might allow the sexuals to "pay back" some of the twofold cost of sex (Vrijenhoek 1984; Bell 1982; Case and Taper 1986). This study, however, has not addressed the issue of relative niche overlap of multiple clones with a sexual species but merely has shown that individual clones have a reduced niche breadth relative to a coexisting sexual species. The FNV model cannot allow sexuals to coexist with a large number of clones because the combined niche breadth of a large clonal assemblage can eclipse that of the sexuals (Vrijenhoek 1979, 1984; Weeks 1993). It is perhaps for this reason that many of the apparently stable *Poeciliopsis* assemblages have been among a sexual species and only a handful of differing clones (Vrijenhoek 1984, 1994).

Acknowledgements

The authors thank A. Varela and R. Schenck for help with the field collections, M. Bartosek and two anonymous reviewers for critically reviewing the manuscript, and R.C. Vrijenhoek for constructive criticism of the design of the study. This study was funded in part by a National Science Foundation doctoral dissertation support grant (BSR-8815423) to SCW.

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Thermal heterogeneity in the hyporheic zone of a glacial floodplain

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Abstract: We examined the thermal regime of surface and hyporheic waters at three kryal sites and four krenal streams within the channel network of a glacial floodplain. Temperature was continuously measured for 1 year in the surface stream and at sediment depths of 30 and 80 cm. The vertical pattern of water temperature was strongly influenced by the direction and intensity of surface water – groundwater exchanges. At sites characterized by strong downwelling of surface waters, the thermal regimes of surface and hyporheic waters were virtually identical. In contrast, inputs of groundwater substantially increased mean summer temperatures in the hyporheic zone of the main kryal channel, decreased summer temperatures in the hyporheic zone of krenal streams, and elevated hyporheic temperatures of all stream types during winter. Groundwater from different sources had dramatically different effects on the seasonal regime of temperature in the hyporheic zone. Inflow of shallow alluvial groundwater had minimal effects on seasonal patterns of hyporheic temperature, whereas upwelling from deep alluvial and hillslope aquifers resulted in significant time lags and differences in seasonal amplitudes between surface and hyporheic temperatures. The unexpectedly high thermal heterogeneity of hyporheic waters presumably sustains biodiversity and stimulates ecosystem processes in this glacial floodplain.

Résumé : Nous avons étudié le régime thermique des eaux superficielles et hyporhéiques à trois sites en aval des glaces et dans quatre ruisseaux de source dans un réseau de cours d'eau d'une plaine d'inondation glaciaire. La température a été mesurée en continu durant une année dans l'écoulement de surface et à des profondeurs de 30 cm et de 80 cm dans les sédiments. Le profil de la température de l'eau est fortement influencé par la direction et l'intensité des échanges entre les eaux de surface et les eaux souterraines. Aux sites caractérisés par une forte descente des eaux de surface, les régimes thermiques des eaux superficielles et hyporhéiques sont presque identiques. En revanche, les apports d'eau souterraine augmentent de façon importante la température estivale moyenne dans la zone hyporhéique du chenal glaciaire principal, diminuent la température estivale dans la zone hyporhéique des ruisseaux de source et font croître la température hivernale dans tous les types de ruisseaux. Les eaux souterraines d'origines différentes produisent des effets bien caractéristiques sur le régime saisonnier de température de la zone hyporhéique. L'arrivée d'eau souterraine d'origine alluviale superficielle a un effet minimal sur l'évolution saisonnière de la température de la zone hyporhéique; au contraire, la remontée d'eau à partir d'alluvions profonds ou d'aquifères des versants des vallées produit des différences d'amplitude saisonnière et des décalages temporels significatifs entre les températures des eaux de surface et celles des eaux hyporhéiques. Cette hétérogénéité thermique élevée et inattendue des eaux hyporhéiques favorise sans doute la biodiversité et stimule le fonctionnement de l'écosystème dans cette plaine d'inondation glaciaire.

[Traduit par la Rédaction]

Introduction

Low temperature is usually considered to be the primary factor responsible for the reduced diversity and distinctive nature of zoobenthos in glacial-fed streams (Ward 1994). Metakryal biotopes, defined as the uppermost reaches of glacial streams where maximum temperatures do not exceed 2°C, are colonized almost exclusively by chironomids in the genus *Diamesa*. The study of thermal heterogeneity in glacial streams is of special interest because an increase in water temperature is expected to promote the diversification of benthic communities. Milner and Petts (1994) proposed a qualitative model that relates longitudinal increases in the benthic diversity of glacial streams to downstream increases in temperature and channel stability. According to the model, *Diamesa* would be the sole or predominant members of the metakryon fauna (maximum temperature < 2°C), but other chironomid genera and black flies (Simuliidae) would be added to the community where maximum temperatures ranged between 2°C and 4°C. Mayflies (Baetidae) and stoneflies (Nemouridae, Chloroperlidae) appear where water temperatures exceed 4°C.

Thermal heterogeneity may be considerably higher in glacial rivers that expand laterally in a braided corridor or a floodplain. Indeed, glacial floodplains comprise a variety of

Received October 22, 1999. Accepted March 28, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 4, 2001.
J15415

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 DOI: 10.1139/cjfas-58-7-1319 © 2001 NRC Canada

aquatic habitats including kryal (glacial-fed), rhithral (snowmelt-fed), and krenal (groundwater-fed) streams, the temperature regimes of which would reflect differences in discharge, water source, and configuration. Ward et al. (1999) showed continuous temperature measurements (5 Aug. to 30 Sept. 1996) conducted in four different channel types of the glacial floodplain of the Roseg River (Switzerland). Daily average temperatures of surface water ranged from 3.5°C to 5.9°C, with maximum instantaneous temperature exceeding 10°C at two sites.

Because most invertebrates colonizing high mountain streams may achieve part of their life cycle within the streambed sediment, hyporheic water temperature may be as important as surface water temperature in determining the diversity of benthic communities. Irons et al. (1989), who examined streambed water temperatures in an Alaskan subarctic stream, suggested that benthic invertebrates may avoid freezing by migrating downward into groundwater-fed areas of the hyporheic zone. However, although temperature patterns within the streambed have been investigated in a variety of streams, including temperate (Evans and Petts 1997), desert (Valett et al. 1990; Constantz and Thomas 1997), arctic (Wankiewicz 1984), and subarctic streams (Irons et al. 1989), we are unaware of any published work reporting on the thermal regime of hyporheic water of a high-mountain stream system.

The objective of this paper is to examine patterns of water temperature in the sediment of kryal and krenal streams of a glacial river – floodplain system and to identify the main factors that generate vertical changes in the thermal regime of stream water. According to the findings of previous investigations (Shepherd et al. 1986; Silliman and Booth 1993; Brunke and Gonser 1997), we expected vertical patterns of water temperature to be strongly influenced by the direction and intensity of surface water – groundwater exchanges. More especially, we hypothesized that groundwater inflow within the streambed would substantially increase hyporheic water temperature of kryal streams in summer and all stream types in winter.

Materials and methods

Study sites

The glacial floodplain of the Roseg River (Bernina Massif of the Swiss Alps) lies at an elevation of 2000 m asl (above sea level) and extends 3.8 km downstream from a glacier terminus. Detailed information on the geomorphological, hydrological,and hydrochemical characteristics of this glacial system were reported by Tockner et al. (1997), Ward et al. (1999), and Malard et al. (1999, 2000). Mean annual river discharge, recorded by the Swiss Hydrological Geological Survey 7.2 km downstream from the floodplain terminus for the period of 1955 to 1997, was 2.76 $m^3 \cdot s^{-1}$. The floodplain is characterized by a predictable monomodal flood pulse. Daily mean discharge peaks during the ice-melting season (from 6 to 10 $m^3 \cdot s^{-1}$ in July and August) and is minimum in winter (ca. 0.2 $m^3 \cdot s^{-1}$ from December to March) when surface flow is sustained solely by groundwater inputs. Aquifers develop in glaciofluvial deposits that extend to a depth of at least 30 m.

Because vegetation on the floodplain surface is sparse, streams are directly exposed to sunlight. The channel network is 21.4 km long in summer and comprises a diverse array of aquatic habitats that differ considerably in their sources of water and degree of hydrological connectivity with the main river. Temperature measurements were conducted from June 1997 to June 1998 in four krenal streams (K1, K2, K3, and K4) and three sites located along the main kryal river (R1, R2, and R3). For comparison with previous works on the hydro-ecology of this glacial river system, krenal streams numbered K1 to K4 in this paper corresponded to codes G-10, G2, G5, and X5 used in previous publications (e.g., Tockner et al. 1997; Malard et al. 1999, 2000). Kryal sites R1, R2, and R3 corresponded to codes M-10, M10, and M12 (see also Table 1 for site concordance between publications).

Krenal streams had no upstream surface connection with glacial meltwater-fed channels since they were fed by shallow alluvial groundwater (streams K1 and K2) or hillslope aquifers (streams K3 and K4) (Tockner et al. 1997; Ward et al. 1999). They had small wetted width (2.6 – 4.4 m), shallow water depth (0.08 – 0.11 m), and discharge typically below 100 $L \cdot s^{-1}$ (Table 1). Surface water was clear and had specific conductance higher than that of kryal segments. Channels K2 and K4 also received glacial water from the main kryal river during summer high-flow periods. The main kryal river, i.e., the primary channel in the floodplain, received most of its flow (>80%) from the valley glaciers during the ice ablation season (from July to September). River discharge averaged 7.2 $m^3 \cdot s^{-1}$ in summer and exhibited marked diel fluctuations. Water depth at kryal sites R1, R2, and R3 averaged 0.25 m and wetted width ranged from 5.8 to 13.0 m (Table 1). The kryal river carried dilute and turbid water (specific conductance, 32–37 $\mu S \cdot cm^{-1}$; turbidity, 116–132 nephelometric turbidity units, NTU). Streambed sediments derived from crystalline rocks of the catchment were composed of an extremely heterogeneous mixture of cobble, pebble, gravel, and sand at all sites.

Site instrumentation

Small piezometers were installed for sampling hyporheic water and recording hyporheic temperature. Each piezometer consisted of a 0.03-m-diameter PVC (polyvinyl chloride) tube with a 0.08-m-long metal tip at its end. The tip was perforated with 3-mm holes, allowing water to circulate freely around the datalogger. Piezometers were introduced by hammering an inner steel bar into the sediment while the PVC tube was protected with an outer metal pipe. Piezometers were installed near the center of krenal streams (sites K1, K2, K3, and K4) at depths of 30 and 80 cm below the streambed. Because bedload transport prevented the installation of a piezometer in the main kryal river, piezometers were placed approximately 2 m away from the water shoreline at sites R1, R2, and R3. Piezometers were sunk 80 cm into the gravel, approximately 30 cm below the surface water – riverbed interface. Although the piezometers were originally installed in the non-wetted area of the channel, surface flow around the pipes was found to occur irregularly in response to the lateral expansion of the river.

Vertical hydraulic gradient and silica concentration

Differences in hydraulic head between hyporheic water and surface water were determined in a manometer by measuring the heights of water columns drawn simultaneously from the piezometers and surface water (Lee and Cherry 1978). Vertical hydraulic gradient was calculated as the differential head (in centimetres) divided by the depth (in centimetres) of the piezometer screen below the sediment–water interface. For piezometers located in the parafluvial zone along the main kryal river, the horizontal hydraulic gradient was calculated as the differential head (in centimetres) divided by the distance (in centimetres) to the shore edge. Negative hydraulic gradients indicated potential downwelling of surface water, whereas positive hydraulic gradients indicated potential upwelling of hyporheic water. Silica concentrations in surface water and hyporheic water were also measured to verify the existence of water exchange indicated by hydraulic gradients and to identify ar-

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Table 1. Mean (±SD) physical, hydrological, and chemical characteristics of the study sites.

Site	Code	Type	Distance[a] (m)	Width[b] (m)	Depth[b] (m)	Discharge ($L \cdot s^{-1}$)	Sp. Cond. ($\mu S \cdot cm^{-1}$)	Turbidity (NTU)
K1	G-10	Krenal	630	2.6 (±0.3)	0.08 (±0.01)	24	53 (±2.1)	25 (±6.4)
K2	G2	Krenal	2530	2.7 (±0.3)	0.09 (±0.01)	40	68 (±3.2)	4 (±0.1)
K3	G5	Krenal	3180	4.4 (±0.5)	0.09 (±0.00)	74	87 (±5.7)	1 (±0.3)
K4	X5	Krenal	2680	3.0 (±0.4)	0.11 (±0.02)	34	61 (±9.5)	6 (±3.9)
R1	M-10	Kryal	630	5.8 (±1.9)	0.24 (±0.04)	7200	32 (±5.6)	132 (±76)
R2	M10	Kryal	2500	7.8 (±1.5)	0.27 (±0.05)	7200	36 (±9.1)	123 (±51)
R3	M12	Kryal	2950	13.0 (±3.3)	0.24 (±0.06)	7200	37 (±9.3)	116 (±56)

Note: Codes correspond to site names used in previous publications. Channel width, water depth, specific conductance (Sp. Cond.), and turbidity (in nephelometric turbidity units, NTU) were measured from July to October 1997 ($n = 4$). Discharge values correspond to single measurements for sites K1, K2, K3, and K4 and to summer average river discharge for sites R1, R2, and R3. SD, standard deviation.

[a]Distance from the glacier terminus.

[b]Width and depth of the wetted channel.

eas of groundwater inflow into the hyporheic zone. Because silica concentration is much higher in groundwater than in surface water of the Val Roseg floodplain (Malard et al. 1999), increase in silica concentration in the hyporheic zone would reflect local groundwater inflow within the streambed. Upwelling of groundwater and downwelling of surface water were expected to occur locally both in krenal and kryal streams, although these streams were classified as groundwater-fed channels and glacial meltwater-fed channels, respectively, based on their main water source (i.e., aquifers and glaciers, see above). Hyporheic water was collected with a peristaltic pump, filtered (Whatman GF/F filters; 0.7 µm), and stored for 1 to 3 days at 4°C before analysis. Silica concentration was measured with the heteropoly blue method. Measurements of vertical hydraulic gradients and silica concentrations were carried out monthly at all sites from February 1997 to January 1998.

Temperature measurement

Surface water and hyporheic water temperatures were recorded using TR Minilog temperature loggers (VEMCO Ltd., Shad Bay, N.S., Canada). These are waterproof, cylindrical dataloggers (dimensions 16 mm × 68 mm) with a protruding stainless steel probe. Based on the manufacturers information, the working range, resolution, and accuracy of the temperature loggers were 24°C (–4–20°C), 0.1°C, and 0.2°C, respectively. Before use, temperature loggers were placed in a water bath, the temperature of which was adjusted within a 7.8°C range (3.6–11.4°C). Variations between temperature measured by the individual units and water bath temperature averaged 0.1°C with a maximum deviation of 0.2°C. Calibration check was repeated at the end of the field experiment to identify potential drift of temperature loggers. Variations between temperature measured by the individual units and water bath temperature (range 8.1–15.2°C) averaged 0.15°C with a maximum deviation of 0.5°C. Consequently, no correction factor was applied to any temperature logger. In the field, temperature was measured at 1-h intervals and dataloggers were downloaded monthly (except during winter) onto a portable computer using an infrared light interface.

The dataloggers used to measure surface water temperatures were secured in a closed stainless steel casing attached to a metal stick driven into the riverbank. The cubic casing (dimensions 14 cm × 5 cm × 5 cm) was filled with water and placed at the water–streambed interface near the center of the stream. This specific design was adopted to prevent the temperature loggers from being swept away or damaged by rapid current and sediment transport that occur during the ice ablation period in the main kryal river as well as in krenal streams (i.e., sites K2 and K4) during major floods. To test the effect of the casing on temperature measurement, surface water temperature was recorded during 10 days in a krenal stream using a logger placed directly on the streambed and a logger protected with housing. Average temperature measured by the loggers during this 10-day recording period (temperature range 3–8.4°C) differed by only 0.1°C and variations between instantaneous temperatures never exceeded 0.6°C (average deviation 0.15°C). Dataloggers used to measure hyporheic water temperature were positioned in the piezometers at the screen depth. All piezometers were hermetically closed with a cap to prevent air circulation within the tube.

Meteorological data, including air temperature (hourly intervals) and snow height (two measures a day), were obtained from the nearest station of the Swiss Meteorological Survey (Samedan, 1705 m asl). Mean annual air temperature for the period 1996–1998 was 1.8°C. Average air temperature over the study period (1 June 1997 – 31 May 1998) was 2.0°C. Average daily temperature peaked in August (maximum daily average 15.7°C) and was minimum in January (minimum daily average –18.0°C). The lowest instantaneous air temperature was –25.0°C on 28 January. The first snowfall occurred on 9 November 1997 and the snow cover persisted over mid-April. Maximum snow height recorded in Samedan was 0.67 m although snow accumulation in the floodplain probably exceeded 1 m.

Data analysis

The absolute value of the difference between silica concentrations of hyporheic water and surface water was computed for each sampling date. One-way analysis of variance (ANOVA) followed by Tukey's multiple comparison test was then used to evaluate differences in the vertical change of silica concentrations between sites. Significant differences between sites would reflect local heterogeneity in surface water – groundwater interactions. When necessary, data were log transformed to meet the assumption of homogeneity of variances. The same procedure was repeated to compare vertical changes in daily mean temperature between sites. In that case, input data corresponded to the absolute values of the differences between daily temperatures of surface water and hyporheic water. Throughout the manuscript, differences between sites were considered significant when $p < 0.05$.

Cross-correlation analysis (Jenkins and Watts 1968; Box and Jenkins 1976) was used to compare temperature patterns of surface and hyporheic waters. The statistical procedure used was described in detail by Mangin (1984, 1994). The cross-correlation corresponds to the correlation of the time series of surface water temperature with the time series of hyporheic water temperature, shifted by a particular number of hourly observations (i.e., k = lag). The cross-correlogram indicates values of the cross-correlation coefficient (r) between surface water and hyporheic water temperatures for increasing values of k (x-axis shifted forward) and $-k$

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(*x*-axis shifted backwards). The cross-correlation coefficient was obtained using the formula proposed by Jenkins and Watts (1968):

$$r_{+k} = \frac{C_{x,y(k)}}{S_x S_y} \text{ with } C_{x,y(k)} = n^{-1} \sum_{i=1}^{n-k} (x_i - \bar{x})(y_{i+k} - \bar{y})$$

$$r_{-k} = \frac{C_{x,y(k)}}{S_x S_y} \text{ with } C_{x,y(k)} = n^{-1} \sum_{i=1}^{n-k} (y_i - \bar{y})(x_{i+k} - \bar{x})$$

and with

$x_1, x_2, \ldots, x_n$ = hourly values of surface water temperature

$y_1, y_2, \ldots, y_n$ = hourly values of hyporheic water temperature

$k = 0, 1, 2, \ldots, m$

$$\bar{x} = n^{-1} \sum_{i=1}^{n} x_i$$

$$\bar{y} = n^{-1} \sum_{i=1}^{n} y_i$$

$$S_x^2 = n^{-1} \sum_{i=1}^{n} (x_i - \bar{x})^2$$

$$S_y^2 = n^{-1} \sum_{i=1}^{n} (y_i - \bar{y})^2$$

Hourly temperatures recorded from 15 June to 1 December 1997 ($n = 4080$) were selected to compare seasonal trends of surface water and hyporheic water temperatures from a maximum number of sites. Only temperature recorded at site K4 were excluded from the analysis because the stream dried up early in October. A 24-h moving average filter was applied to the original time series to remove diel thermal fluctuations. Each point in the transformed series was calculated as the mean of 24 adjacent points. Cross-correlation was then computed on the transformed time series using a lag (k) of 8 h and a maximum number of lags (m) of 125. As recommended in the literature (Mangin 1984), the maximum number of lags was determined so that $m \cdot k \leq n/3$.

Hourly temperatures recorded from 15 June to 15 August 1997 ($n = 1488$) were then selected to compare daily patterns of surface water and hyporheic water temperatures at all sites. A first-order differencing was applied to the original time series to remove its trend component. This filter replaced the original time series by its variation: $\hat{x}_{(t)} = (x_t - x_{t-1})$ with $\hat{x}$ = term of the filtered time series and x_t = term of the original time series. Cross-correlation was then computed on the transformed time series using $k = 1$ h and $m = 125$. The lag time between surface and hyporheic temperature patterns was calculated as the number of lags between the highest correlation value and the origin of the cross-correlogram. This lag time was used to determine the diel amplitude of hyporheic water temperature, i.e., for $k = 2$ h, the diel thermal amplitude was calculated as the largest difference between the 24 temperature values measured from 2:00 AM. The relation between diel thermal amplitudes of surface water and those of hyporheic water was examined using Pearson's correlation coefficient. Damping of diel thermal amplitude at depth beneath the stream was computed as the mean difference between diel amplitudes of surface and hyporheic water. One-way ANOVA followed by Tukey's multiple comparison test was then used to evaluate differences in attenuation of diel thermal amplitude between sites.

Results

Hydraulic gradients and vertical patterns of silica concentrations

Most hydraulic gradients measured from February 1997 to January 1998 were negative, indicating a potential downwelling of surface water within the streambed (Fig. 1). Negative gradients were particularly strong at sites K1, K2 (depth of 30 cm), and R1 (depth of 80 cm). Positive hydraulic gradients, and thereby potential upwelling of hyporheic water, were only detected at sites K3 (depth of 80 cm) and K4. The latter site exhibited a clear seasonal change: gradients were negative in spring and autumn and positive in summer.

Increase in silica concentration with increasing depth beneath the streambed was observed at most of the sites at least during some parts of the year (Fig. 1). Vertical patterns of silica were not always consistent with indications provided by vertical hydraulic gradients. For example, there was a marked increase in silica concentration at a depth of 80 cm at site R1, whereas negative hydraulic gradients suggested a downward flow of surface water into the sediment. One-way ANOVA and Tukey's multiple comparison test performed on data collected from May to September 1997 ($n = 6$) revealed significant differences in the vertical change of silica concentrations between sites. Average differences in silica concentrations between surface and hyporheic waters at sites K1, K2 (depth of 30 cm), and R3 were below 0.12 mg·L^{-1} SiO_2. These differences were not statistically different from each other but they were significantly lower than those measured at all other sites. Indeed, the average difference ($n = 6$) in silica concentration between surface and hyporheic waters at sites K2 (depth of 80 cm), K3, K4, R1, and R2 ranged from 0.9 to 1.9 mg·L^{-1} SiO_2; they were not significantly different from each other.

Changes of daily average temperatures at depth beneath the streams

Hourly records of surface water and hyporheic water temperatures are shown in Fig. 2. Gaps in the temperature series of sites K2, K4, and R2 were solely due to drying up of the streams. Surface water temperature at site K2 suddenly decreased in August because the krenal stream became connected to the main kryal river. One-way ANOVA and Tukey's multiple comparison test performed on daily temperatures measured in summer (from July to September 1997, $n = 92$) revealed significant differences in the vertical change of daily mean temperatures between sites (Table 2). Average differences between daily temperatures of surface and hyporheic water did not exceed 0.3°C at sites showing little vertical increase in silica concentration (i.e., sites K1, K2 at depth of 30 cm, and R3). These differences were not statistically different from each other but they were significantly lower than those measured at sites where hyporheic water was enriched in silica. Indeed, decreases in daily mean temperature at depth beneath the streambed of krenal sites K2 (at depth of 80 cm from 1 July to 14 August 1997), K3,

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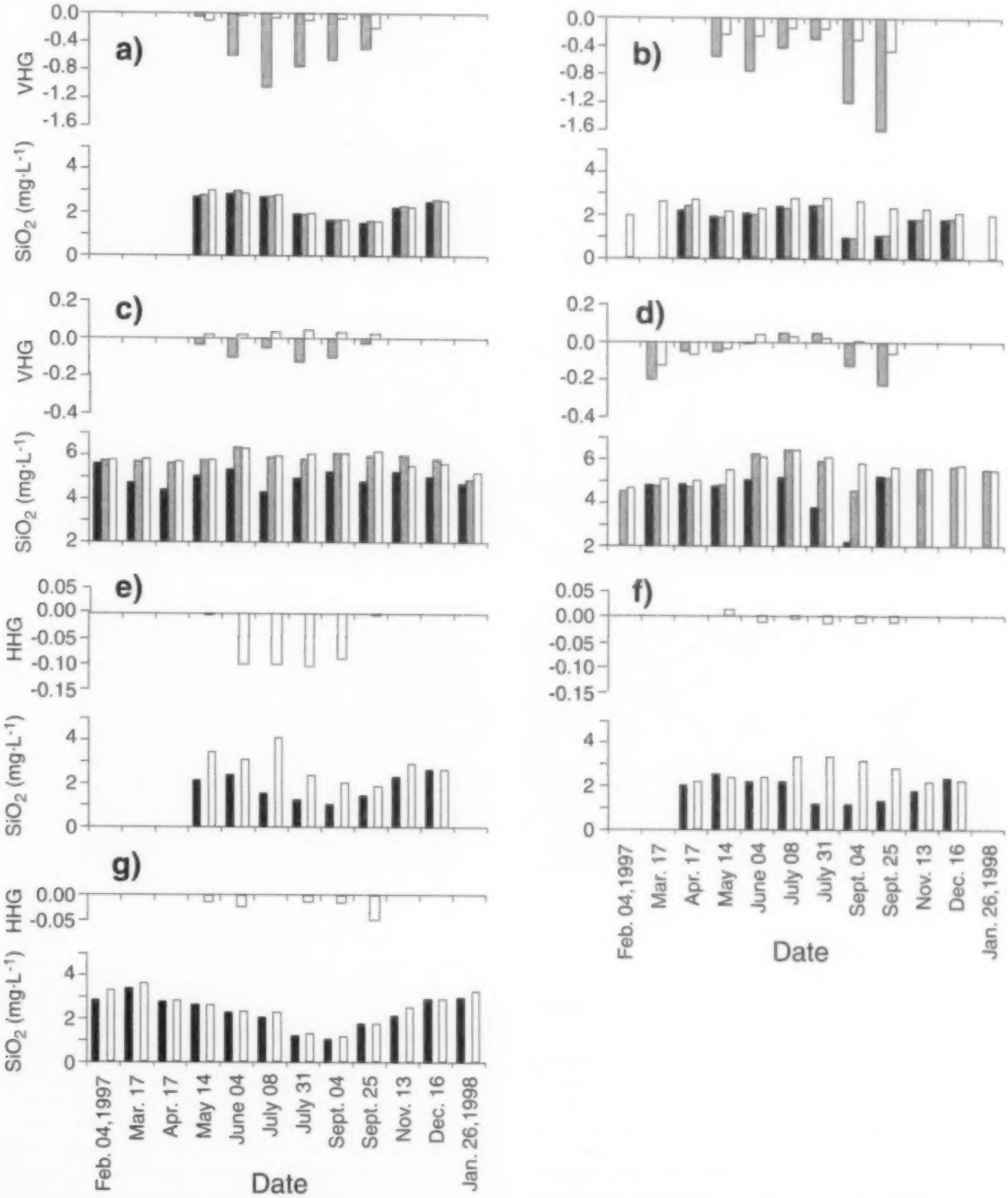
Fig. 1. Hydraulic gradients (cm·cm^{-1}) and silica concentrations (mg L^{-1}) measured at sites located in krenal streams K1, K2, K3, and K4 (*a–d*) and kryal streams R1, R2, and R3 (*e–g*) of the Val Roseg floodplain. VHG and HHG indicate vertical and horizontal hydraulic gradients, respectively. Black, grey, and white patterns correspond to measures carried out in the surface stream and at depths of 30 cm and 80 cm, respectively, into the streambed.



and K4 ranged from 1.0 to 2.8°C (Table 2). Inversely, daily mean temperature of hyporheic water was higher than that of surface water at kryal sites K2 (at depth of 80 cm from 1 July to 14 Aug. 1997), R2, and R1. At the latter site, daily temperature of hyporheic water reached a maximum of 7.3°C on 1 July while daily temperature of surface water

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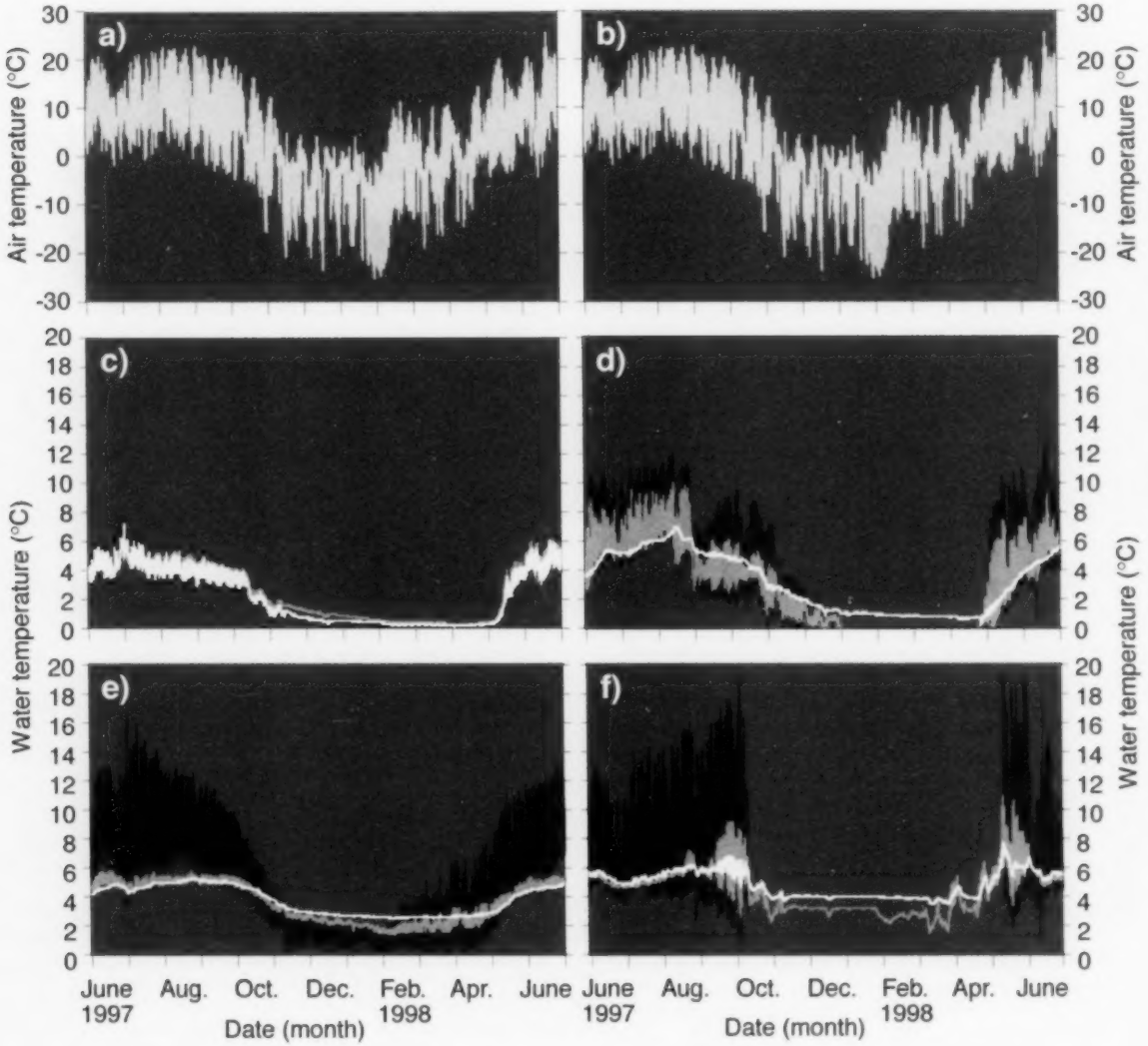
Fig. 2. Temperature records for the water column and sediment at sites located in krenal streams K1, K2, K3, and K4 (*c–f*) and kryal streams R1, R2, and R3 (*g–i*) of the Val Roseg floodplain. Air temperature (*a* and *b*) is from the nearest station of the Swiss Meteorological Survey (Samedan, 1705 m asl). Black, grey, and white lines indicate water temperature measured in the surface stream and at depths of 30 and 80 cm, respectively, into the streambed.



was only 1.2°C. From July to September, surface water accumulated only 97 degree-days above 0°C while hyporheic water accumulated 374 degree-days.

Differences in the vertical pattern of winter daily temperatures between sites could not be evaluated statistically because three sites lacked either hyporheic or surface flow. Average winter temperatures of surface water and hyporheic water ranged from 0.3 to 1.1°C (mean 0.6°C ± 0.4) and from 0.4 to 4.0°C (mean 1.5°C ± 1.2), respectively (Table 2). Daily mean temperature of hyporheic water exceeded that of surface water by at least 0.5°C at four sites (K2, K3, K4, and R3). Although minimum air temperature reached –25°C, hyporheic temperature at a depth of 80 cm into the sediment of sites K3 and K4 remained above 2.5°C and 3.8°C throughout the winter. Winter degree-day sums in the hyporheic zone of these two sites ranged from 180 to 356 while surface water in most of the channels accumulated less than 50 degree days.

Cross-correlation between surface and subsurface temperature patterns

Seasonal trend

Results of the 24-h moving average smoothing of air, surface water, and hyporheic water temperature series recorded from 15 June to 1 December 1997 (n = 4080) are shown in Fig. 3. The temporal variability in the transformed time series included not only a seasonal trend but also short-term thermal fluctuations, the period of which was different from a multiple of 24 h. The seasonal patterns of surface water

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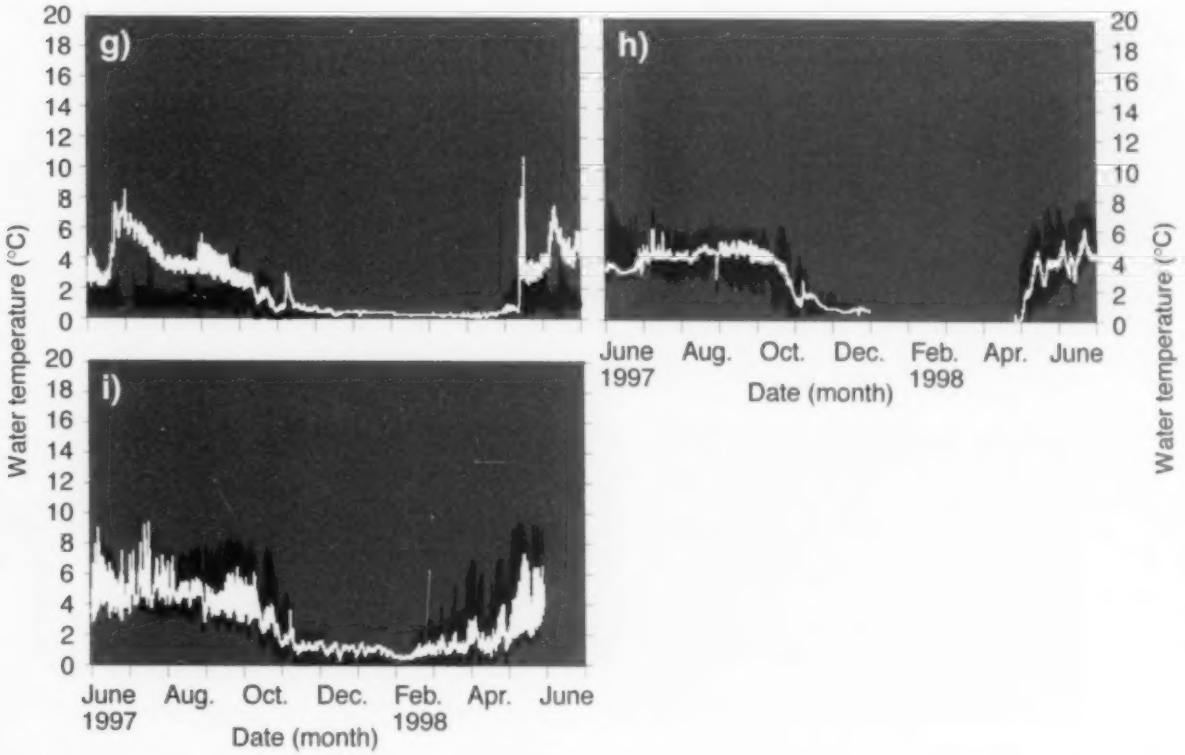
Fig. 2. (*concluded*).



and hyporheic water temperatures were strongly correlated at all sites (Fig. 4). The cross-correlation coefficient ranged from 0.76 to 0.99 for $k = 0$ and slowly decreased as the number of lags increased. However, the shape of the cross-correlograms differed markedly among sites. The cross-correlograms of sites showing little vertical increase in silica concentration (i.e., sites K1, K2 at depth of 30 cm, and R3) were almost symmetrical about the *y*-axis. This implied that there was almost no phase difference (i.e., higher than 8 h) between the seasonal patterns of surface and hyporheic water temperatures. In contrast, all cross-correlograms of sites characterized by steep vertical gradients of silica were asymmetrical about the lag of 0. The rising limb of the correlogram was much steeper than the declining limb at sites K2 (depth of 80 cm), K3, and R2, indicating that the seasonal pattern of hyporheic temperatures lagged behind that of surface temperature. However, the number of lags separating the highest correlation value from the origin of the cross-correlogram could not be used to evaluate the seasonal lag between surface and hyporheic temperature patterns. Indeed, the time series was too short (less than an annual period) for the cross-correlogram to provide a satisfactory estimate of the seasonal lag. Moreover, the cross-correlation coefficient was not only influenced by the seasonal trend of temperature but also by short-term fluctuations in the transformed time series. Examination of the transformed time series showed that the seasonal peak of surface water temperature at site K2 (i.e., on 12 August) was delayed by a period of about 4 days at a depth of 80 cm into the streambed (Fig. 3). The lag time between the seasonal patterns of surface and hyporheic water temperatures was even more pronounced at sites K3 and R2. Autumnal decline of surface water temperature at site K3 began by mid-August while hyporheic temperature remained constant until the end of September. Stream temperature at site R2 started to decline by the end of August while hyporheic water temperature leveled off until the end of September. This late decline in hyporheic temperature coincided with the appearance of a steep vertical gradient of SiO_2 concentration (Fig. 1).

The cross-correlogram of site R1 was also asymmetrical about the *y*-axis but its declining limb was steeper than its rising limb (Fig. 4). The asymmetry indicated that the seasonal pattern of surface water temperature lagged behind that of hyporheic temperature. Examination of the transformed time series revealed that hyporheic water temperature peaked on 23 June and then continuously decreased towards the winter (Fig. 3). Surface water temperature also reached a maximum at the end of June (25 June) but the autumnal decline of temperature only began at the end of September. The rapid vernal rise of hyporheic temperature at site R1, which was recorded during two consecutive years, did not correspond to an increase in air temperature. This particular seasonal pattern was not site specific because it was also observed at krenal site K1, which was located only 50 m away from site R1 (Fig. 3). Although the slope of the correlogram for site R1 was steeper for increasing values of k than for increasing values of $-k$, the cross-correlation coefficient peaked for positive values of k (i.e., $k = 6$ or 48 h; Fig. 4). This implied that although the seasonal pattern of surface temperature was more inertial than that of hyporheic

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Table 2. Vertical changes in daily mean temperature (±SD).

		Summer		Winter	
Site	Depth	Mean	Change[a]	Mean	Change[a]
K1	0 cm	4.0 (±0.6)	—	0.3 (±0.1)	—
	30 cm	4.3 (±0.4)	+0.2 (±0.2)	0.7 (±0.3)	+0.4 (±0.2)
	80 cm	4.1 (±0.5)	+0.1 (±0.1)	0.4 (±0.1)	+0.1 (±0.1)
K2[b]	0 cm	6.9 (±0.6)	—	0.4 (±0.3)	—
	30 cm	6.9 (±0.6)	0.00 (±0.2)	0.5 (±0.3)	+1.0 (±0.2)
	80 cm	5.8 (±0.5)	−1.0 (±0.5)	1.4 (±0.2)	+1.0 (±0.2)
K2[c]	0 cm	4.4 (±1.2)	—		
	30 cm	4.6 (±1.1)	+0.2 (±0.2)		
	80 cm	5.5 (±0.6)	+1.1 (±0.8)		
K3	0 cm	7.8 (±1.0)	—	1.1 (±0.3)	—
	30 cm	5.1 (±0.2)	−2.7 (±1.0)	2.0 (±0.3)	+0.9 (±0.3)
	80 cm	5.0 (±0.2)	−2.8 (±1.0)	2.7 (±0.1)	+1.6 (±0.3)
K4	0 cm	6.6 (±0.8)	—	—	—
	30 cm	5.6 (±0.6)	−1.0 (±0.9)	3.0 (±0.3)	—
	80 cm	5.7 (±0.4)	−1.0 (±0.8)	4.0 (±0.1)	—
R1	0 cm	1.1 (±0.1)	—	0.3 (±0.1)	—
	80 cm	4.1 (±1.1)	+3.0 (±1.1)	0.4 (±0.1)	+0.1 (±0.1)
R2[d]	0 cm	3.8 (±0.4)	—	0.9 (±0.2)	—
	80 cm	4.5 (±0.3)	+0.7 (±0.4)	0.7 (±0.1)	−0.2 (±0.2)
R3	0 cm	4.5 (±0.5)	—	0.3 (±0.3)	—
	80 cm	4.7 (±0.7)	+0.3 (±0.5)	0.9 (±0.3)	+0.6 (±0.2)

Note: Unless specified, summer and winter temperatures were measured from July to September 1997 (n = 92) and from December 1997 to February 1998 (n = 90), respectively. SD, standard deviation.

[a]Mean difference in daily temperature = [(daily temperature of hyporheic water (HW) temperature − daily temperature of service water (SW) temperature)/n].

[b]Summer temperatures from 1 July to 14 August 1997 (n = 47). Winter temperatures from 1 to 29 December 1997 (n = 29).

[c]Summer temperatures from 15 August to 30 September 1997 (n = 45).

[d]Winter temperatures from 1 to 15 December 1997.

temperature, short-term variations of temperature in the hyporheic zone lagged behind that of surface water temperature. Temperature of surface water effectively reached a maximum before that of hyporheic water during short-term thermal fluctuations that occurred in October and November (Fig. 3).

Diel fluctuations

Cross-correlation between daily patterns of surface and hyporheic temperatures and vertical damping of amplitude differed markedly among sites (Table 3, Fig. 5). Daily thermal patterns were strongly correlated at krenal sites exhibiting little vertical decrease in silica concentration (i.e., sites K1 and K2 at a depth of 30 cm). Cross-correlation coefficients peaked for lag times less than or equal to 1 h ($r_{+k} \sim 0.7$). Because of weak vertical damping of surface water temperature fluctuations (from 0.5 to 1.9°C), the average diel amplitude of hyporheic water temperature was higher than 1°C. Diel amplitudes of surface and hyporheic water temperatures were strongly correlated ($r \sim 0.9$).

The cross-correlation coefficient was typically less than 0.1 at krenal sites characterized by steep vertical gradients of silica concentration (i.e., sites K2 at a depth of 80 cm, K3 at a depth of 80 cm, and K4) (Fig. 5). The average diel amplitude of hyporheic water did not exceed 0.2°C and the differences between diel amplitudes of surface and hyporheic temperatures were high, ranging from 4.0 to 6.2°C (Table 3). Tukey's multiple comparison tests indicated that these differences were not statistically different from each other but they were significantly higher than those measured at all other sites, except site K3 (at a depth of 30 cm). At the latter site, the daily pattern of hyporheic temperature was correlated with that of surface water temperature, the cross-correlation coefficient being maximum ($r_{+k} = 0.55$) for a lag time of 4 h. Diel amplitudes of surface and hyporheic water temperatures were significantly correlated ($r = 0.68$), despite a strong reduction in diel thermal amplitude of hyporheic water (i.e., 5.7°C).

Maximum cross-correlation coefficients ranged from 0.21 to 0.38 at kryal sites (i.e., sites R1, R2, and R3). Lag times between daily patterns of surface water and hyporheic temperatures were rather similar (7–9 h), although vertical gradients of silica concentration were shown to differ markedly among sites. Despite relatively long lag times, the differences between diel amplitudes of surface and hyporheic temperatures did not exceed 1.8°C. Hyporheic water temperatures still exhibited substantial diel amplitudes ranging from 0.4 to 1.7°C. For example, the attenuation of thermal amplitudes of surface water was 1.9°C at site K2 (lag time = 1 h) but only 0.4°C at site R1 (lag time = 9 h) (Table 3). Diel amplitudes of surface and hyporheic water temperatures were poorly correlated ($r < 0.3$), the correlation being not even statistically significant at site R2. On several occasions, the diel thermal amplitude of hyporheic water was found to

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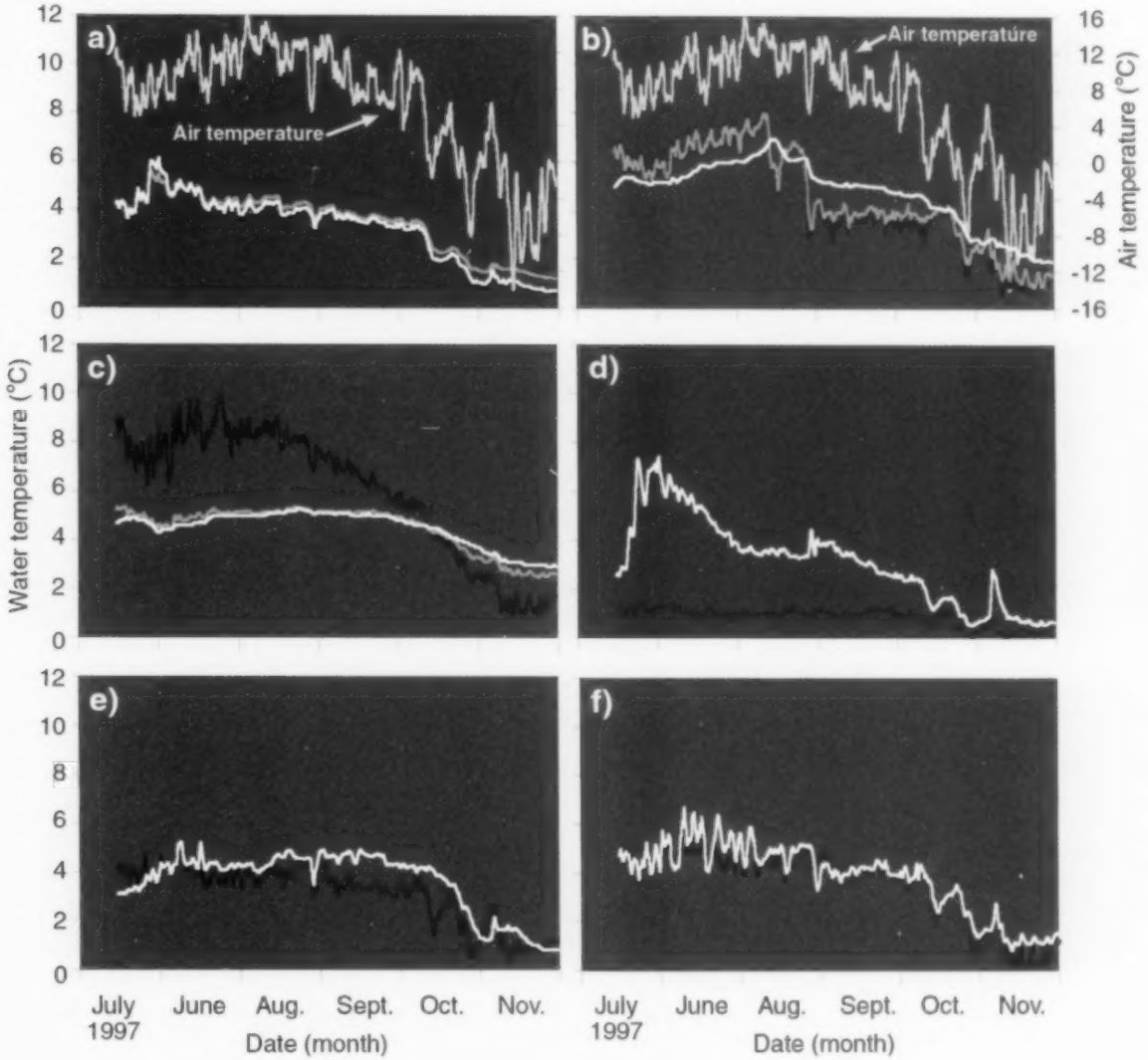
Fig. 3. Moving average smoothing (24-h) of air, surface water, and hyporheic water temperature series recorded at sites located in krenal streams K1, K2, and K3 (*a–c*) and kryal streams R1, R2, and R3 (*d–f*) of the Val Roseg floodplain. Air temperature (*a* and *b*) is from the nearest station of the Swiss Meteorological Survey (Samedan, 1705 m asl). Black, grey, and white lines indicate water temperature measured in the surface stream and at depths of 30 cm and 80 cm, respectively, into the streambed.



be higher than that of surface water. From 23 to 26 June, diel amplitude of hyporheic water temperature at site R3 was on average 2.4°C higher than that of surface water temperature.

Temporal changes in cross-correlation between daily patterns of surface and subsurface water temperatures

Seasonal shifts in the vertical changes of diel regime of surface temperature were examined using data from site K4 (Fig. 6). Six periods were identified based on the direction of water exchanges between the stream channel and the hyporheic zone, the presence–absence of surface flow, and the presence–absence of a snow cover on the dry streambed. In summer (period *a* in Table 4 and Fig. 6), the surface stream was flowing and gaining water from the hyporheic zone. Early autumn (period *b*) was a period of decreasing discharge and declining groundwater table during which the surface stream was losing water into the bed sediment. By the middle of October (period *c*), the streambed was completely dry and directly exposed to atmospheric conditions. Snow fell in November and covered the streambed until the end of March (period *d*). Periods *e* (neither snow cover nor surface flow) and *f* (surface flow and downwelling flow pattern) had the same characteristics as periods *c* and *b*, respectively, but they took place in spring while the groundwater table was rising. Cross-correlation between transformed time series (first-order differentiation) of surface and hyporheic temperatures was performed for each period using a lag of

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Fig. 4. Cross-correlograms between transformed time series (24-h moving average filter) of surface and hyporheic temperatures recorded at sites located in krenal streams K1, K2, and K3 (*a*–*c*) and kryal streams R1, R2, and R3 (*d*–*f*) of the Val Roseg floodplain. Hourly temperature data are from 15 June to 1 December 1997 (n = 4080). Thick line represents surface water versus hyporheic water at a depth of 30 cm. Thin line represents surface water versus hyporheic water at a depth of 80 cm.

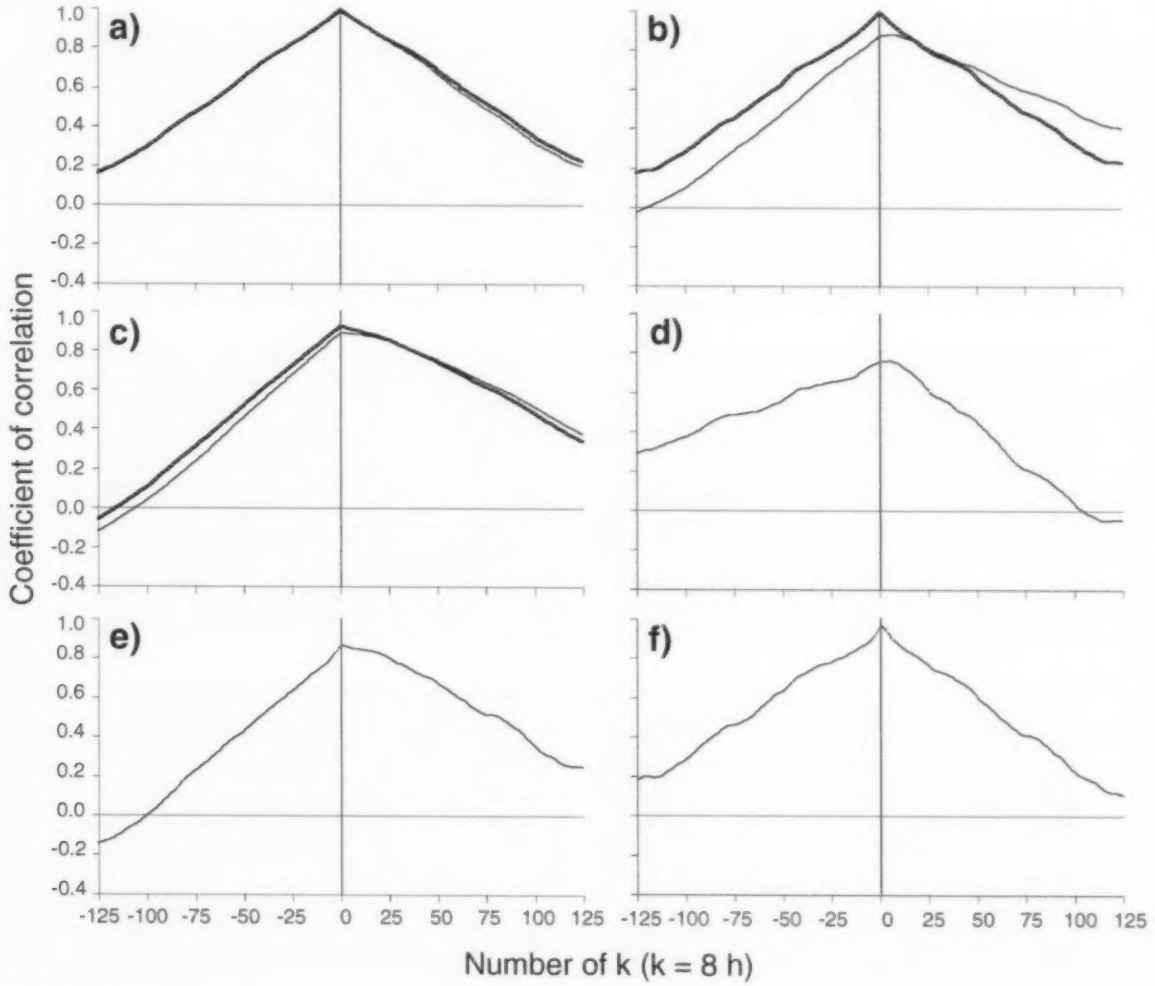

Table 3. Lag times between daily patterns of surface and hyporheic temperatures and damping of diel amplitudes into the bed sediment of krenal and kryal streams. Daily temperatures were measured from 15 June to 15 August 1997 (n = 62).

	Surface	Hyporheic water (30 cm)				Hyporheic water (80 cm)			
Sites	Amp.	Lag	Amp.	Red.	r	Lag	Amp.	Red.	r
K1	1.6 (±0.5)	<1	1.0 (±0.4)	–0.6 (±0.2)	0.93*	1	1.1 (±0.4)	–0.5 (±0.2)	0.90*
K2	4.1 (±1.4)	1	2.2 (±1.0)	–1.9 (±0.7)	0.89*	na	0.1 (±0.1)	–4.0 (±1.4)	0.10
K3	6.2 (±2.0)	4	0.5 (±0.2)	–5.7 (±1.8)	0.68*	na	0.0 (±0.1)	–6.2 (±2.0)	0.10
K4	6.1 (±2.5)	na	0.1 (±0.1)	–5.9 (±2.4)	0.28*	na	0.2 (±0.1)	–5.9 (±2.4)	0.50*
R1	1.2 (±0.6)					9	0.8 (±0.4)	–0.4 (±0.6)	0.26*
R2	2.3 (±1.0)					9	0.4 (±0.4)	–1.8 (±1.0)	0.24
R3	2.8 (±1.6)					7	1.7 (±0.2)	–1.1 (±1.7)	0.26*

Note: Amp., mean diel amplitude (in °C); Lag, lag time (in hours) between surface and hyporheic temperature patterns; Red., mean reduction in diel amplitude = [(diel amplitude of SW temperature – diel amplitude of HW temperature)/n]; r, Pearson's correlation coefficient between diel amplitudes of SW and HW temperatures; asterisks indicate significant correlations ($p < 0.05$); na, not applicable.

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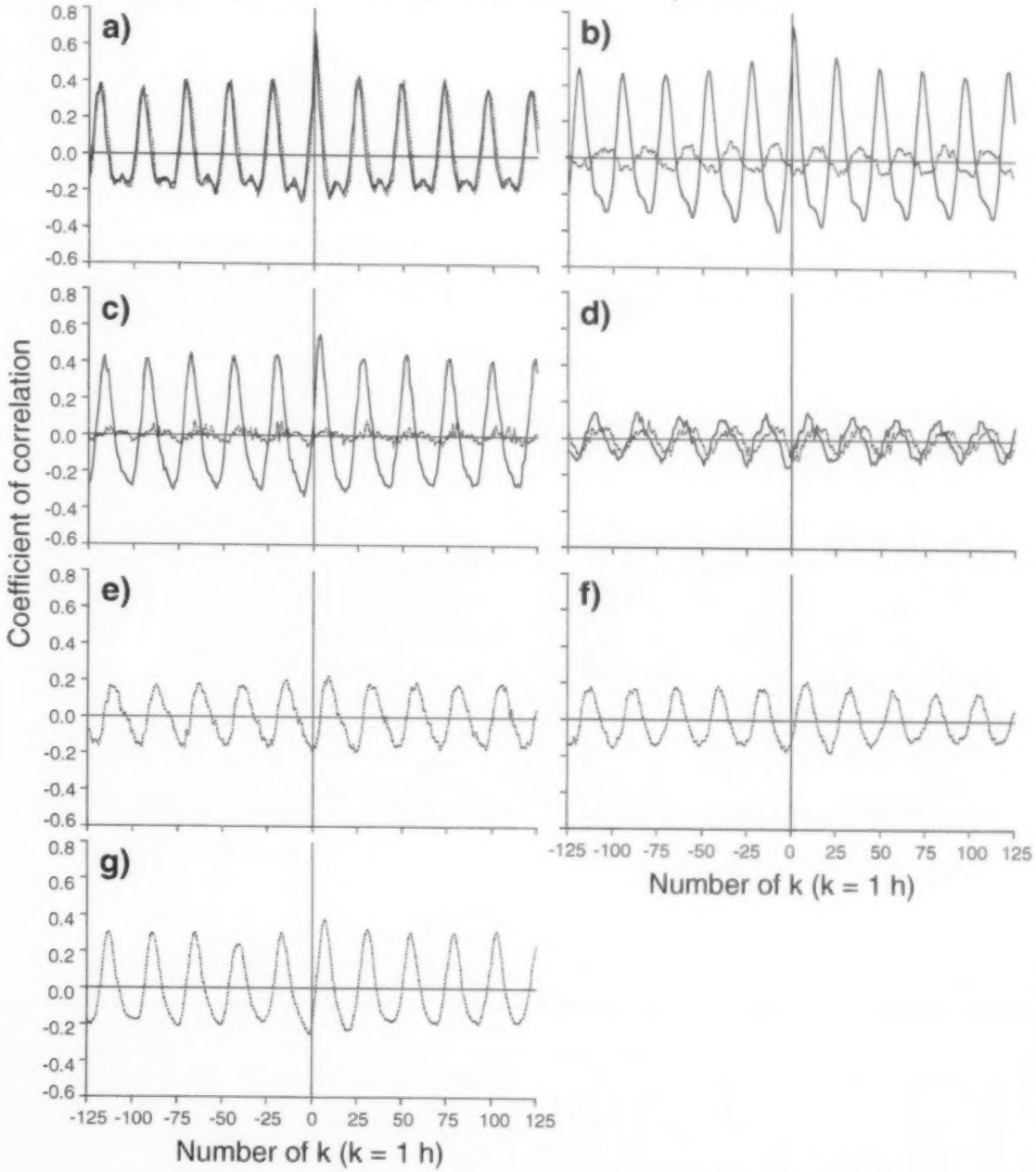
Fig. 5. Cross-correlograms between transformed time series (first-order differentiation) of surface and hyporheic temperatures recorded at sites located in krenal streams K1, K2, K3, and K4 (*a*–*d*) and kryal streams R1, R2, and R3 (*e*–*g*) of the Val Roseg floodplain. Hourly temperature data are from 15 June to 15 August 1997 (n = 1488). Solid line represents surface water versus hyporheic water at a depth of 30 cm. Broken line represents surface water versus hyporheic water at a depth of 80 cm.



1 h and a maximum number of lags of 125 (Fig. 7). The number of hourly observations (n) for a particular period varied from 432 to 3456 (Table 4). Air temperature was used as an input series instead of surface water temperature when the stream lacked surface flow (periods *c*, *d*, and *e*).

There was no dependence between temperature series of surface and hyporheic water during periods of upwelling flow (Fig. 7*a*). In contrast, daily patterns of surface and hyporheic temperatures were strongly correlated when stream water downwelled into the bed sediment (Fig. 7*b* and 7*f*). However, infiltration of surface water had dissimilar effects on the temperature pattern of hyporheic water in au-

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Fig. 6. Time series of snow height, air temperature, and surface and hyporheic water temperatures recorded at krenal site K4. Snow height and air temperature were measured at the nearest station of the Swiss Meteorological Survey (Samedan, 1705 m asl). (*a–f*) Periods for which cross-correlation was performed between daily patterns of surface and hyporheic temperatures.

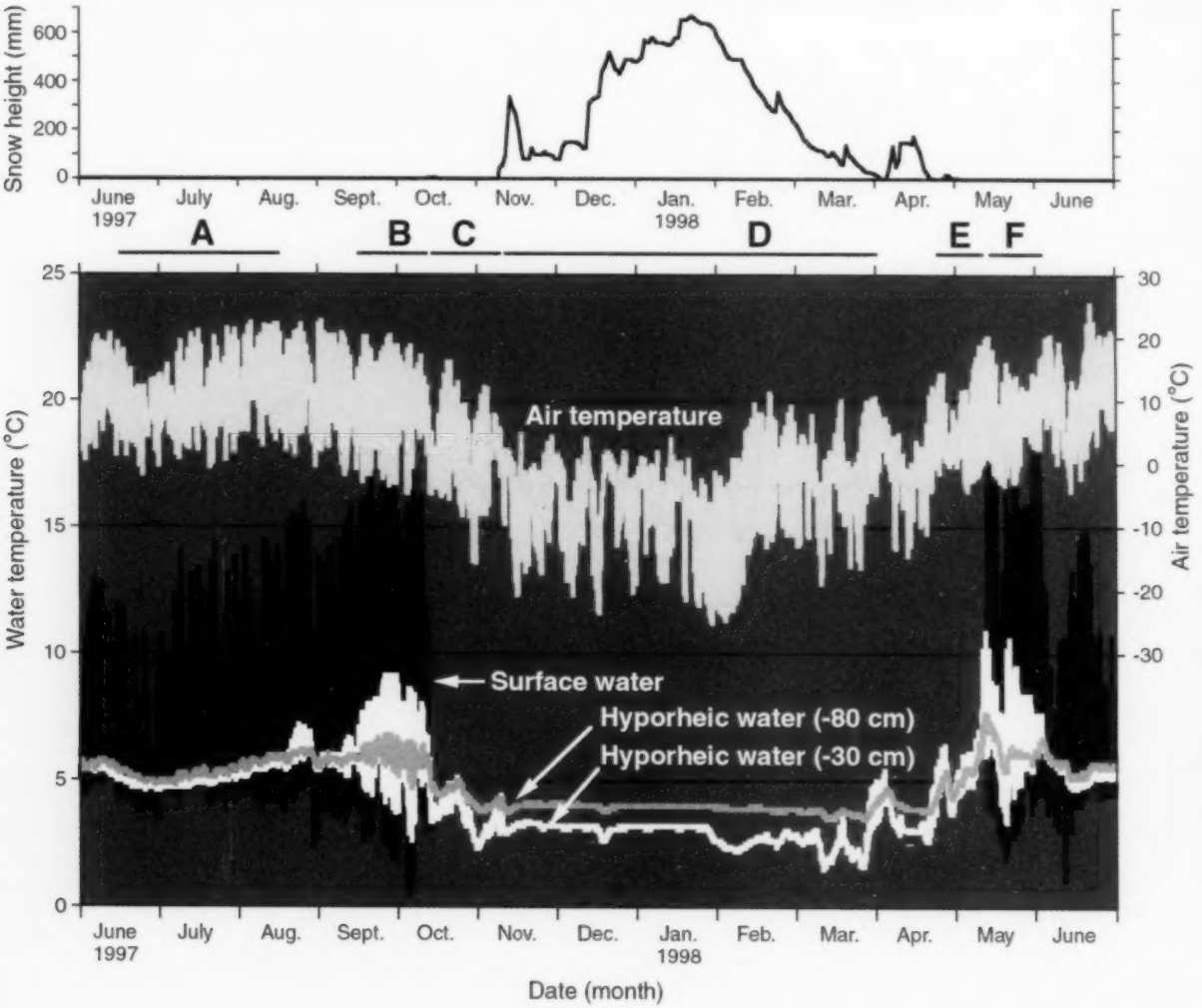

Table 4. Lag times between daily patterns of surface and hyporheic temperatures and damping of diel amplitudes (±SD) into the streambed sediment at site K4.

Periods	Surface flow	Snow cover	VHG	Surface Amp.	Hyporheic water (30 cm) Lag	Amp.	*r*	Hyporheic water (80 cm) Lag	Amp.	*r*
(*a*) 15 June – 15 Aug. 1997 (*n* = 62)	yes	no	+	6.1 (±2.5)	na	0.1 (±0.1)	0.28*	na	0.2 (±0.1)	0.50*
(*b*) 15 Sept. – 10 Oct. 1997 (*n* = 26)	yes	no	–	12.3 (±3.5)	4	3.5 (±1.4)	0.90*	6	0.9 (±1.4)	0.82*
(*c*) 13 Oct. – 9 Nov. 1997 (*n* = 28)	no	no	na	13.1 (±6.0)	8	0.6 (±0.3)	–0.04	na	0.2 (±0.1)	–0.05
(*d*) 10 Nov. – 2 Apr. 1998 (*n* = 144)	no	yes	na	12.8 (±5.3)	na	0.2 (±0.3)	0.07	na	0.0 (±0.1)	–0.02
(*e*) 23 Apr. – 10 May 1998 (*n* = 18)	no	no	na	11.2 (±5.3)	8	1.1 (±0.4)	0.67*	na	0.4 (±0.3)	0.50*
(*f*) 13 May – 2 June 1998 (*n* = 21)	yes	no	–	12.0 (±3.0)	2	3.2 (±1.5)	0.38*	na	0.3 (±0.2)	0.24

Note: Recording periods are those indicated in Fig. 6. In the absence of surface flow (periods *c*, *d*, and *e*), diel amplitude of air temperature was calculated. Amp., mean diel amplitude (in °C); Lag, lag time (in hours) between surface and hyporheic temperature patterns; Red., mean reduction in diel amplitude = [(diel amplitude of SW temperature – diel amplitude of HW temperature)/*n*]; *r*, Pearson's correlation coefficient between diel amplitudes of SW and HW temperatures; asterisks indicate significant correlations ($p < 0.05$); na, not applicable.

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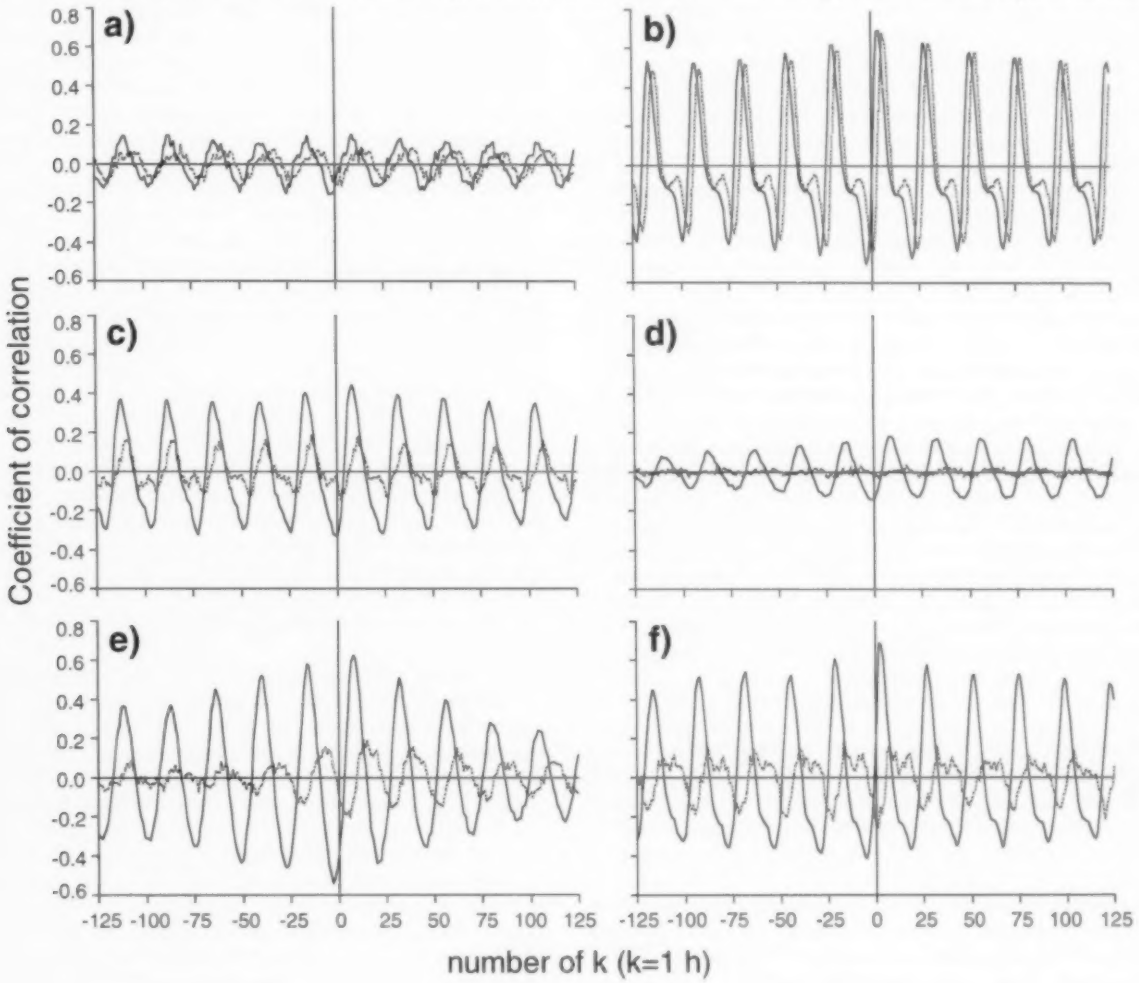
Fig. 7. Cross-correlograms between transformed time series (first-order differentiation) of surface and hyporheic temperatures recorded at sites K4. (*a–f*) Periods for which cross-correlation was performed between daily patterns of surface and hyporheic temperatures. In the absence of surface flow (*c–e*), daily patterns of air temperature were used for the cross-correlation with hyporheic water temperature. Solid line represents surface water (*a*, *b*, and *f*) or air (*c*, *d*, and *e*) temperature versus hyporheic water temperature at a depth of 30 cm; broken line represents surface water (*a*, *b*, and *f*) or air (*c*, d, and *e*) temperature versus hyporheic water at a depth of 80 cm.



tumn and spring (Table 4). Although the lag time at a depth of 30 cm into the sediment was longer in autumn (4 h) than in spring (2 h), the diel amplitudes of hyporheic water temperature were similar (i.e., 3.5°C in autumn and 3.2°C in spring for a diel amplitude of surface water of about 12°C). Moreover, downwelling flow of surface water resulted in diel fluctuations of hyporheic water temperatures at a depth of 80 cm only in autumn.

Temperature of hyporheic water at a depth of 30 cm into the sediment was found to exhibit diel fluctuations in the absence of surface flow and snow cover (periods *c* and *e* in Table 4 and Fig. 6). Daily patterns of hyporheic and air temperatures were cross-correlated, the cross-correlation coefficient being maximum (r_{+k} = 0.45 in autumn, 0.62 in spring) for lag times of 8 h. Thermal diel amplitudes of hyporheic water averaged 1.1°C in spring and were significantly correlated (r = 0.67) with diel amplitudes of air temperature. Cross-correlation between hyporheic and air temperatures was lost (r_{+k}max = 0.18) and diel fluctuations of hyporheic water were no longer detectable when the streambed became covered by snow (period *d* in Table 4 and Fig. 7). From 10 November 1997 to 10 March 1998, hyporheic water temperature at a depth of 80 cm into the sediment remained high (average = 4.0°C; n = 2904) and extremely constant (±0.1°C) despite cold (average = –6.7°C) and fluctuating (±7.0°C) air temperatures.

Discussion

Vertical heterogeneity of water temperature in the floodplain

River–floodplain systems, which comprise diverse surficial

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waterbodies lateral to the main stream, exhibit a high degree of thermal heterogeneity. Differences in temperature between water bodies of a temperate river floodplain typically exceed 15°C in summer (Mosley 1983; Brunke and Gonser 1997). In addition, glacial river systems are characterized by a pronounced longitudinal gradient of temperature because surface water in the main kryal stem warms up as distance from the glacier terminus increases (Milner and Petts 1994). The present study demonstrated that thermal heterogeneity along the vertical dimension of a glacial floodplain could be as high as along lateral and longitudinal dimensions. The maximum differences between instantaneous temperatures of different surficial water bodies in the floodplain reached 15.9°C in summer and 3.8°C in winter. Remarkably, instantaneous measurements of surface and hyporheic water temperatures at a given site could differ by as much as 12.1°C in summer and 2.7°C in winter over a distance of only 80 cm. Average summer temperature of hyporheic water at a distance of only 630 m from the snout of the glacier (4.1°C at site R1) was higher than surface water temperature recorded 2500 m downstream of the glacier terminus (3.8°C at site R2).

Considerable variations were also observed among sites in the vertical changes of the thermal regime of surface water. As pointed out by Ward and Stanford (1982), the thermal regime of aquatic habitats is a composite of patterns of absolute temperatures, seasonal and diel amplitudes, and rates of change. In addition to the comparison of absolute temperatures of surface and hyporheic waters, cross-correlation analysis was used to examine vertical changes in the seasonal and diel patterns of temperature. Results showed that each of the seven sites investigated in this study exhibited a distinctive vertical pattern of temperature.

Influence of local surface water – groundwater exchanges on hyporheic water temperature

Temperature of hyporheic water is determined by conductive and convective heat transport, which is influenced by a number of physical, thermal, and hydrodynamic parameters (Suzuki 1960). Conduction of heat at depth beneath the stream depends on the thermal properties of the streambed sediment (Lapham 1989). Convective transport of thermal energy into the hyporheic zone is due to the flow of infiltrating stream water and groundwater (Silliman and Booth 1993). Because thermal properties of the sediment were not measured during this study, we cannot exclude the possibility that differences in the vertical patterns of temperature among sites are in part attributable to thermal conduction. However, the correspondence between the vertical patterns of SiO_2 concentration and temperature strongly suggests that surface water – groundwater exchanges exert a dominating influence on the temperature of hyporheic water. Bundschuh (1993) calculated that convection was more than 90% of the total heat transport in groundwater at a Darcy velocity of 20 $m \cdot year^{-1}$. This is the order of magnitude for water velocity that would be expected for coarse sediments of the glacial floodplain of the Roseg River. As expected, local upwelling and downwelling flow patterns, which were more likely caused by site-specific hydraulic or geomorphologic conditions, occurred in both krenal and kryal channels investigated during this study.

Thermal regime of hyporheic water under conditions of strong downwelling

The temperature regimes of surface and hyporheic water were almost identical at sites where hydraulic gradients and vertical patterns of SiO_2 concentrations indicated a strong local infiltration of surface water (i.e., sites K1, K2 at a depth of 30 cm, and R3). The average daily temperature of hyporheic water equaled that of surface water and the seasonal and diel amplitudes of surface temperature exhibited little attenuation beneath the streambed. Constantz and Thomas (1997) obtained similar results from a 2-year continuous measurement of temperature beneath an influent stream in New Mexico, U.S.A. The authors measured substantial diel thermal fluctuations (from 4 to 8°C) beneath the stream, with relatively little differences in amplitude at depths of 30, 105, and 300 cm. However, in most studies on temperature patterns within streambeds, thermal fluctuations of surface water were strongly attenuated with increasing depth from the infiltration site (Silliman et al. 1995; Evans and Petts 1997; Ronan et al. 1998). Low thermal gradients and substantial diel amplitudes measured in the hyporheic zone at sites K1 and K2 probably reflected a rapid convective transport of thermal energy via downwelling flow of surface water. The lag time between diel patterns of surface and hyporheic temperatures was only 1 h at depths ranging from 30 to 80 cm. Assuming convective transport of heat and subvertical flow of surface water, water velocity into the sediment would be in the order of 10^{-4} $m \cdot s^{-1}$.

Effect of groundwater input on average temperature of hyporheic water

Groundwater inflow within the streambed, as indicated by vertical gradients of SiO_2 concentrations, resulted in substantial differences between the patterns of surface and hyporheic temperatures. However, the vertical change in daily average temperature was dependent on the season and stream type. Because surface water of krenal streams warmed up in summer in response to increasing air temperature, inflowing groundwater resulted in a marked decline of hyporheic water temperature. Summer cooling of hyporheic temperature in groundwater-fed areas of lowland streams has already been documented by several authors (Hendricks and White 1991; Silliman and Booth 1993). In contrast, input of groundwater warmed up hyporheic water at kryal sites, which are fed by glacial meltwater throughout summer. In winter, inflow of groundwater increased hyporheic temperature independently of the stream types because surface water temperature fell below 1°C in all floodplain water bodies. In the present study, average winter temperatures of hyporheic water at sites influenced by groundwater input (i.e., sites K3 and K4) were 1–3°C higher than surface water temperature.

Groundwater influence on seasonal patterns of hyporheic water temperature

The seasonal pattern of hyporheic temperature in groundwater-fed sediments of lowland streams is expected to be strongly attenuated and to lag behind that of surface temperature (Shepherd et al. 1986). However, temperature records from the glacial floodplain of the Roseg River showed that the vertical change in the seasonal thermal regime varied markedly among sites as a function of stream type, ground-

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water source, and timing of groundwater inflow. Based on the results of a detailed study of water chemistry in the Val Roseg floodplain, Ward et al. (1999) and Malard et al. (1999) identified three distinct types of groundwater reservoirs within the catchment: (*i*) shallow alluvial groundwater fed mainly by infiltration of stream water on the floodplain surface, (*ii*) hillslope groundwater recharged by snowmelt water in spring and ice-melt water from hanging glaciers in summer, and (*iii*) deep groundwater. The physico-chemical variability and residence time of water within these three reservoirs differed markedly as indicated by the results of groundwater dating carried out at three representative sites of the floodplain in February 1998 using the tritium–helium-3 (^3H–^3He) dating method (Malard et al. 1999). Groundwater ages in shallow alluvial, hillslope, and deep aquifers were 0.4 years ± 0.5 (detection limit of the dating method), 3.7 years ± 0.5, and 26.1 years ± 1.4, respectively (U. Beyerle, ETH/EAWAG, CH-8600 Duebendorf, Switzerland, unpublished data). Groundwater from these different sources probably had dramatically different effects on the seasonal regime of temperature in groundwater-fed areas of the hyporheic zone. Inflow of shallow alluvial groundwater at site K2 resulted in a relatively short lag time (i.e., 4 days) and a small difference in seasonal amplitude (2.6°C) between surface and hyporheic temperatures. In contrast, the lag time and the reduction in seasonal amplitude were much greater at sites influenced by hillslope groundwater. Indeed, the autumnal decline of temperature was delayed by a period of approximately 1.5 months at site K3 and the seasonal amplitude of hyporheic water was 6.6°C less than that of surface water.

The seasonal pattern of hyporheic temperature at site R1 was likely caused by an upward movement of deep groundwater. The steep vernal rise of hyporheic temperature in spring at this site (up to 10.7°C in 1998) was attributed to the infiltration of snowmelt water displacing warm groundwater stored in alluvial sediment of the valley floor during winter. Soil-stored heat might also contribute to the warming of hyporheic water. Kobayashi (1985) showed that spring temperatures of 3–4°C in northern Hokkaido (Japan) streams completely insulated by snow cover was caused by the runoff of subsurface water being warmed up in soils of the catchment. Input of groundwater into the hyporheic zone of the main kryal river at a distance of only 630 m from the glacier terminus had unexpected consequences. First, the annual amplitude of temperature was higher in the hyporheic zone than in the stream and, second, the autumnal decline in hyporheic temperature preceded that of surface temperature. The similarity between the seasonal regimes of temperatures at two nearby sites (K1 and R1) suggested that deep groundwater had a general influence on shallow subsurface temperature in this glacial floodplain.

Multiple factors affecting diel fluctuations of hyporheic water temperature

Diel thermal fluctuations of hyporheic water were found to vary among sites and seasons in response to several factors. As already reported in other studies (Shepherd et al. 1986; Silliman and Booth 1993), diel fluctuations were either absent or strongly attenuated in areas of the hyporheic zone receiving a significant input of groundwater (sites K2 at depth of 80 cm, K3, and K4). In the floodplain of the Roseg River, groundwater inflow within the streambed resulted in a maximum difference in thermal amplitude between surface and hyporheic water of 17.1°C (site K4 on 5 October 1997).

Irrespective of the source of water, diel thermal fluctuations were recorded at all sites in the parafluvial zone of the main kryal river (sites R1, R2, and R3). The comparative analysis of surface and hyporheic patterns showed that these diel thermal fluctuations could not be caused by convective transport of heat alone. Rather, they probably reflected the percolation of incoming water through sun-exposed gravels of the riverbanks. Several authors, who found summer temperature in the lateral portions of the hyporheic zone to exceed that of stream water, evoked the potential role of atmospheric heat conduction through sun-exposed areas of the riverbed (Shepherd et al. 1986; Valett et al. 1990).

The successive influence of surface water – groundwater exchanges, direct exposure of the streambed to atmospheric conditions, and insulation by snow cover resulted in distinct seasonal changes in diel thermal fluctuations of hyporheic temperature at site K4. Seasonal changes in surface water – groundwater exchanges could even cause diel fluctuations of surface and hyporheic temperature to reach their maxima at different periods of the year. Indeed, despite strong variations in stream discharge (from 30 to 200 $L \cdot s^{-1}$) caused by periodic upstream connections to the main kryal river, inflow of groundwater prevented any diel fluctuation of hyporheic temperature throughout summer. Diel thermal fluctuations in the hyporheic zone peaked in autumn and spring when surface water downwelled into the sediment. However, the thermal effect of infiltrating stream water was less important in spring than in autumn, probably because of a stronger input of groundwater occurring during recharge of hillslope aquifers with snowmelt water. Following drying of the stream in autumn, diel thermal fluctuations persisted in response to the diurnal heating and nocturnal cooling of streambed sediment directly exposed to atmospheric conditions. Fluctuations became undetectable as the streambed was covered by snow, showing that winter loss of thermal heat in the hyporheic zone was limited by the presence of a deep snow cover. Several studies have emphasized the significance of snow cover on temperature and biological activity in the soil zone of winter-cold environments (Coulson et al. 1995; Kennedy and Sharatt 1998). Taniguchi (1985) demonstrated that snow cover played only a negligible role on groundwater temperature at depths exceeding 10 m below the soil surface in a winter-cold region of Japan. Further investigations are needed to determine the extent to which the persistence of snow cover throughout winter may truncate the annual cycle of heat exchange between surface and shallow subsurface environments, thereby elevating hyporheic temperatures throughout winter in the glacial floodplain of the Roseg River.

Ecological implications

The findings of this study demonstrate that, although the primary importance of temperature in stream ecology is widely recognized, a broader perspective is needed. River ecosystems are characterized by environmental gradients along three spatial dimensions (Ward 1989). Longitudinal

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changes in biotic communities along the course of rivers has served as a central theme in stream ecology, with temperature ascribed a major role by both the universal zonation scheme (Illies and Botosaneanu 1963) and the river continuum concept (Vannote et al. 1980). Thermal heterogeneity along the lateral dimension of alluvial floodplains has received much less attention and was not even considered in the zonation or continuum concepts. The few previous studies of temperature along the vertical dimension, reviewed herein, were not intended as comprehensive investigations of subsurface thermal regimes. Therefore, the high vertical thermal heterogeneity documented in the Val Roseg was not anticipated, especially in a glacial floodplain, but appears to explain the existence of a relatively diverse and abundant fauna in this harsh alpine environment (Ward et al. 1999; Burgherr and Ward 2000; Klein and Tockner 2000).

Temperature effects the ecology of aquatic ectotherms through influences on growth and development, life histories, behavior, and competitive hierarchies, all of which determine community composition, species diversity, and abundance levels (Ward and Stanford 1982). Because vertical temperature patterns in the Val Roseg floodplain differ as a function of site and season, aquatic animals at different locations–depths, or cohorts whose active stages occur at different times, may be exposed to quite different thermal conditions. Irons et al. (1993) showed experimentally that invertebrates in Alaskan streams actively moved away from an advancing freeze front, thereby demonstrating the ability to select microhabitats that do not freeze. Given the steep temperature gradient within the alluvium of Val Roseg, by moving less than a metre within substrate interstices, invertebrates can markedly alter the thermal regime to which they are exposed. This places into question the definition of the metakryal as the zone in a glacier stream where maximum temperatures do not exceed 2°C and which, therefore, contains a fauna restricted to chironomids of the genus *Diamesa* (Ward 1994). Although this may be valid for glacial streams that lack extensive floodplains and alluvial aquifers, the presence of Plecoptera and Ephemeroptera only 630 m from the glacier terminus (Burgherr and Ward 2000) may be linked to the particular thermal regime of the hyporheic water.

Acknowledgements

Data included in this paper were collected while the senior author was a member of the Department of Limnology at the EAWAG, Duebendorf, Switzerland. This work was supported by the Swiss National Science Foundation (SNF grant 21-49243.96). Data for characterizing stream morphology and hydrology were kindly provided by P. Burgherr. The authors are indebted to T. Boesch, R. Illi, and B. Ribi for their professional support with the field and laboratory work. The authors also thank D. d'Hulst for his invaluable help with the time-series analysis software (Stochastos) and Mr. Testa and his crew at the Roseg Hotel for their hospitality and the communes of Pontresina and Samedan for providing access to the sampling area.

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Movement and harvesting mortality of American lobsters (*Homarus americanus*) tagged inside and outside no-take reserves in Bonavista Bay, Newfoundland

Sherrylynn Rowe

Abstract: To determine the potential effectiveness of no-take reserves in sustaining fisheries for American lobster (*Homarus americanus*), lobster movement and survival were quantified both within and outside of two no-take reserves in Bonavista Bay, Newfoundland, during 1997–1999. Most (58.7%) tagged lobsters were recaptured in the immediate vicinity of their original capture location. Among lobsters that moved, 77.1% traveled less than 1000 m. Lobster movement resulted in some exchange between no-take reserves and nearby harvested areas (8.7% of lobsters recaptured were in an area different from their location of tagging). Overall, little evidence was found for a relationship between lobster movement and sex, size, or time at large. Annual harvesting mortality accounted for up to 71.9% for lobsters eligible for harvest. However, many more lobsters tagged outside of no-take reserves were harvested (11.5–71.9%) than those tagged in no-take reserves (0.0–18.5%), a result of low frequency of movement between these areas. No difference was found between female and male mortality as a result of the fishery. Because the frequency of lobster emigration from reserves was relatively low and harvesting pressure outside of reserves was intense, results suggest that no-take reserves can offer increased survival to lobsters and thereby may provide benefits to fisheries.

Résumé : Afin de vérifier le rôle potentiel des réserves sans captures (où toute cueillette est interdite) dans le maintien des pêches aux Homards d'Amérique (*Homarus americanus*), les déplacements et la survie des homards à l'intérieur et à l'extérieur de deux de ces réserves dans la baie de Bonavista, Terre-Neuve, ont été quantifiés en 1997–1999. La plupart des homards marqués (58,7%) ont été repris dans le voisinage immédiat du lieu de leur première capture. De plus, 77,1% de ceux qui s'étaient déplacés avaient parcouru moins de 1000 m. Ces déplacements ont généré un certain nombre d'échanges entre les réserves et les zones de pêche adjacentes (8,7% des homards repris se retrouvaient dans une région différente du point de leur marquage). En gros, il existe peu de preuves de l'existence d'une relation entre le déplacement, d'une part, et le sexe, l'âge et le temps écoulé depuis la libération, d'autre part. La mortalité annuelle due à la pêche affectait jusqu'à 71,9% des homards de taille réglementaire. Cependant, à cause de la basse fréquence des déplacements entre ces régions, beaucoup plus de homards marqués à l'extérieur des réserves (11,5–71,9%) que de homards marqués dans les réserves (0,0–18,5%) ont été capturés. Il n'y avait pas de différence dans les mortalités dues à la pêche chez les mâles et chez les femelles. Ces résultats indiquent que, comme l'émigration des homards hors des réserves est relativement faible et que la pression de la pêche à l'extérieur des réserves est intense, les réserves sans captures favorisent la survie accrue des homards et peuvent ainsi être bénéfiques aux pêches commerciales.

[Traduit par la Rédaction]

Introduction

Marine no-take reserves, areas closed to harvesting, increasingly are being used to conserve exploited populations and sustain fisheries but there have been few assessments of whether they achieve the goals for which they were created. In the presence of intense harvesting pressure, no-take reserves may minimize over-exploitation by making part of the population inaccessible. It has been shown that abundance, mean size of individuals, and spawning biomass of portions of exploited populations residing inside no-take reserves are often greater than in comparable areas subjected to harvesting (reviewed by Roberts and Polunin 1991; Rowley 1994). These differences are expected because many fish and invertebrates live longer, reach larger body size, and produce considerably more eggs in the absence of harvesting mortality (Bohnsack 1992, 1996; Roberts and Polunin 1993). Proximate success of any reserve will depend on individuals therein having greater survival than those outside and in the presence of intense local harvesting pressure, this will largely depend on reserve size in relation to individual movement. Empirical data concerning populations' responses to local protection are urgently needed, and yet there have been few studies (reviewed by Roberts and Polunin 1991; Rowley 1994). Moreover, most investigations

Received September 20, 2000. Accepted April 17, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 4, 2001.
J15982

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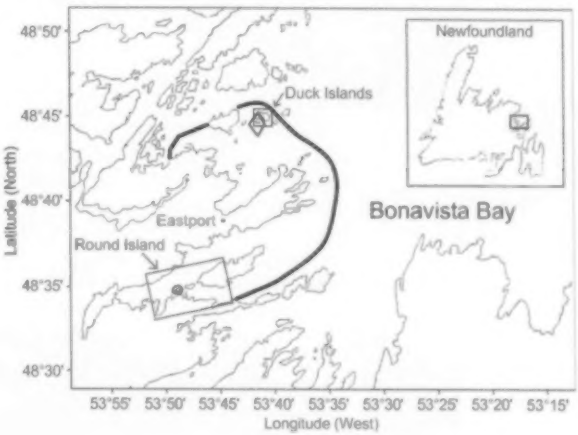
 DOI: 10.1139/cjfas-58-7-1336 © 2001 NRC Canada

have made only static comparisons of population parameters such as abundance and individual size between reserves and nearby harvested areas and do not adequately address the causes of any differences that may exist between them.

Canada's Fisheries Resource Conservation Council (FRCC 1995) has raised concerns about the future of American lobster (*Homarus americanus*) stocks in Canada. Lobsters are long-lived, benthic invertebrates characterized by slow growth, late maturation, long intervals between matings, and egg production that increases exponentially with increasing female size (Aiken and Waddy 1980*a*, 1980*b*; Ennis 1981). In many areas, exploitation rates are high (harvesters take up to 85% of animals present that are eligible for legal harvest each year) and primarily immature individuals are taken, resulting in low levels of population egg production (estimated to be as low as 1–2% of that expected in an unfished population) and increased risk of recruitment failure (FRCC 1995). The FRCC (1995) indicated that increases in egg production, reductions in exploitation rate, and improvements in population structure were necessary. No-take reserves might be useful in achieving conservation objectives, but because of intense harvesting pressure on surrounding lobster grounds, they could only be effective if adult movement occurred at a sufficiently low rate to permit increased adult survival. Furthermore, reserves must be of sufficient size to protect a significant portion of the population. In some parts of their range, such as the waters around Newfoundland, adult American lobsters are rather localized in their movements (e.g., Ennis 1984*a*, 1984*b*) and may be ideal candidates for reserve protection.

Around the Eastport Peninsula, in Bonavista Bay, Newfoundland (Fig. 1), the local lobster grounds consist of a narrow band of rocky substrate that extends from the mainly 5- to 10-m-high cliff shoreline to depths generally less than 25 m at 25–100 m offshore. In this area, the lobster harvesting season lasts about nine weeks, usually beginning in early May. Harvesters fish close to their home ports using small open boats and conventional wooden-lathed traps. Each harvester is permitted to set 200 traps, which are deployed in depths of less than 20 m and checked every 1–2 days. Ovigerous females and lobsters less than 82.5 mm in carapace length (CL) are protected from exploitation. During 1997, in response to a decline in local lobster landings and the FRCC (1995) findings, Eastport Peninsula harvesters established two no-take reserves for lobster conservation, one at Round Island and one at Duck Islands (Fig. 1). The reserves encompassed a marine area of 2.1 km^2 that surrounded three small islands and extended beyond the rocky substrate typically used by lobsters. Because local harvesters implemented and enforced the reserves, issues of illegal harvesting were avoided (Rowe and Feltham 2000). I employed capture–mark–recapture techniques to quantify movement and survival of adult lobsters between reserves and surrounding harvested areas at Round Island and Duck Islands. Specifically, my objectives were to (*i*) assess lobster movement (frequency of movement, distance traveled among lobsters that moved, and frequency of emigration from, and immigration to, no-take reserves) and whether it was related to time at large, sex, or size and (*ii*) determine the vulnerability of lobsters to harvest in relation to tagging area (no-take reserves versus nearby harvested areas) and sex.

Fig. 1. Eastport Peninsula Lobster Management Area (boundary shown by thick black line) with study site (box) and no-take reserve boundary (thin black line) at Round Island and Duck Islands.



Materials and methods

Assessing lobster habitat and movement

A combination of a Global Positioning System (GPS; Trimble Explorer II with differential correction using a surveyed base station offering ±1 m accuracy) and a Geographic Information System (GIS; SPANS with digitized data from 1 : 12 500 aerial photographs georeferenced using a digital terrain model with ±30 m accuracy for Round Island area and digitized 1 : 50 000 topographic maps prepared by Energy, Mines and Resources Canada with ±100 m accuracy for Duck Islands area) was used to map lobster habitat within no-take reserves and surrounding areas subjected to harvesting. Lobster habitat was defined by local ecological knowledge of Eastport Peninsula lobster harvesters; shallow water areas (<20 m) with rocky substrate were typically deemed appropriate. The shoreline was considered to be the inner boundary of the habitat and the outer boundary was defined as the farthest distance from shore that harvesters could set a conventional trap during the harvesting season and expect to catch lobsters, usually where the nearshore bottom sloped rapidly into deeper water. Geographic co-ordinates of the outer habitat boundary were determined from a boat operated at slow speed and directed by local harvesters while position fixes were obtained every few seconds using the GPS. Habitat boundary co-ordinates were overlaid onto topographic maps of the region using the GIS.

Subsequently, local lobster habitat was divided into small zones that were defined by obvious physical landmarks (e.g., one zone might consist of the lobster habitat within a small cove; Figs. 2 and 3). Such zone definition was necessary because harvesters would provide much of the recapture information and finer resolution was not possible with this approach. These zones would form the level of accuracy to which I would assign individual lobster locations. The midpoint of each zone was located on topographic maps by eye using the average of estimates from four different observers (Figs. 2 and 3). The distance that a lobster moved was considered to be the minimum distance from the midpoint of the zone of origin to the midpoint of the zone of termination, across the sea surface. Distances were calculated using the GIS and maps described above.

Biological sampling during fall

During 23 September to 3 October 1997, after reserves had been established for several months (including one harvesting season

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Fig. 2. Lobster habitat at the Round Island site. Each zone of lobster habitat and its midpoint (black cross) are shown, as well as regions comprising no-take lobster reserve area (Round Closed; dark gray), nearby harvested area used as control (Round Open; medium gray), and other nearby areas open to harvesting but not covered during fall research trapping (white).

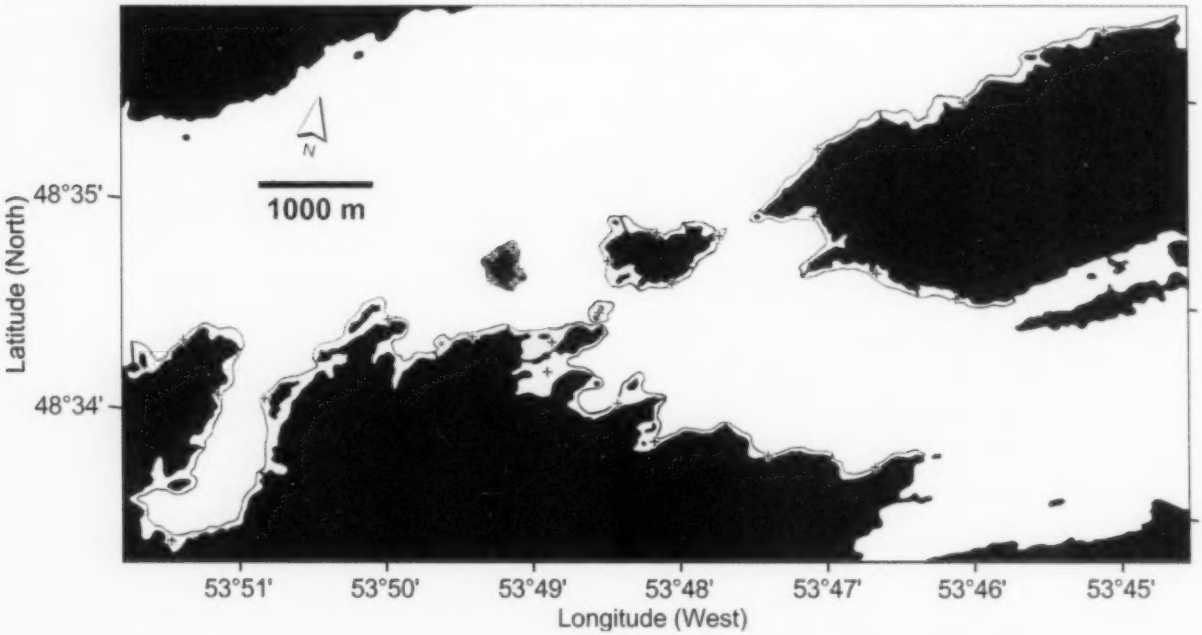
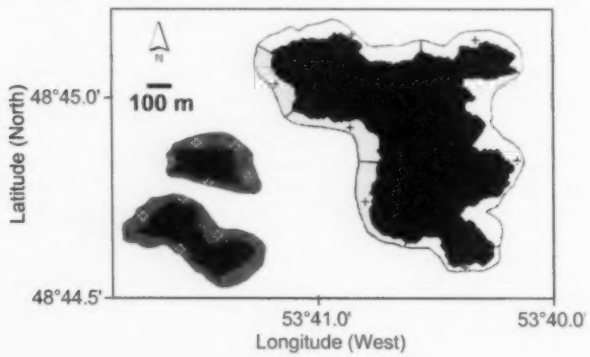


Fig. 3. Lobster habitat at the Duck Islands site. Each zone of lobster habitat and its midpoint (black cross) are shown, as well as regions comprising no-take lobster reserve area (Duck Closed; dark gray), nearby harvested area used as control (Duck Open; medium gray), and other nearby areas open to harvesting but not covered during fall research trapping (white).



and one molting period), lobsters within and outside of no-take reserves (Figs. 2 and 3) were captured, marked, and released. Harvesters who had trapped lobsters in the areas before closure assisted with research fishing, using their own boats and conventional traps. During research fishing, 25 traps were set inside each of the two reserves (hereafter referred to as Round Closed and Duck Closed) and 25 traps were set in each of two nearby harvested areas (hereafter referred to as Round Open and Duck Open). Traps were checked every day (weather permitting). For each lobster captured, zone of capture was recorded, carapace length was measured using vernier calipers, sex and shell condition (i.e., new versus old; Ennis 1977) were determined, and reproductive condition of females (i.e., ovigerous or non-ovigerous) was noted. Also, each lobster was marked with an individually numbered streamer tag that was easily visible to potential observers. Because conventional traps typically did not retain lobsters <65 mm CL, most individuals sampled were above this size.

This protocol was repeated during fall 1998 (26 September to 9 October, although no measurements or tagging occurred on 9 October) and fall 1999 (6 to 15 September). In addition, during 1998 and 1999, some fall recaptures at the Round Island site were made by underwater observation using SCUBA (19 to 24 August 1998 and 23 August to 1 September 1999) and by catch-and-release research trapping using traps designed to target juvenile lobsters (28 September to 3 October 1998) in the general tagging area.

Biological sampling during spring

During 1998 (4 May to 5 July) and 1999 (3 May to 9 July), recapture efforts were made primarily by the commercial harvest ongoing in areas surrounding the reserves (covering a large geographic area), although underwater observation using SCUBA as well as catch-and-release research trapping using traps designed to target juvenile lobsters were also used in the general tagging area at the Round Island site.

Before each harvesting season, a major public awareness and advertising campaign was conducted to maximize participation of harvesters in reporting marked lobsters. Letters were sent to all lobster harvesters in the Eastport area describing the project, providing instructions for handling marked lobsters and returning tag information, and asking for cooperation. Local harvesters were extremely supportive of the research and provided the information requested (Rowe and Feltham 2000). If eligible for legal harvest, marked lobsters captured in the fishery were retained by harvesters for me to examine; otherwise, information was recorded by harvesters at sea and the lobster was released close to the site of capture.

All lobsters caught during spring recapture periods were examined for streamer tags. Upon capturing a marked individual, tag

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number, carapace length, sex, shell condition, and zone of capture were noted. If the marked lobster was not eligible for legal harvest and was observed only by the harvester, size was noted as above or below the minimum legal size (82.5 mm CL).

Analyzing lobster movement patterns

Although multiple recaptures were common, only the first recapture for each individual lobster was considered for analyses concerning movement. Lobsters were recaptured either during the fall research trapping period in which they were tagged (Fall 1, 1–13 days post-tagging), during the next spring commercial fishery (Spring 1, 209–282 days post-tagging), during the next fall research trapping period (Fall 2, 324–379 days post-tagging), during the spring commercial fishery approximately 1½ years later (Spring 2, 580–644 days post-tagging), or during the fall research trapping period approximately 2 years later (Fall 3, 704–721 days post-tagging). This presented some complications for the analyses because (*i*) lobsters were recaptured during periods that were separated by long time intervals and (*ii*) commercial harvesting (and hence sampling) occurred intensely over a large geographic area during spring, whereas sampling effort during fall was less intense and restricted to a relatively small geographic area. Differences in movement patterns among recapture periods were determined using contingency tests for frequency data (i.e., frequency of movement between zones and frequency of immigrants within no-take reserves and nearby harvested areas) and analysis of variance (ANOVA) combined with post hoc Fisher's pairs least significant difference (PLSD) tests for continuous data. Generally, recapture periods were combined when possible for analyses concerning sex and size (see Results).

I analyzed tagging or recapture areas and some recapture periods separately (see Results) to assess the relationship of sex and size (sublegal sized, ≤82 mm carapace length, versus commercial sized, ≥83 mm carapace length) on movement. Frequency data were analyzed using a generalized linear model with binary response variables (moved versus did not move and immigrant versus non-immigrant) using a logit link function. Continuous data were analyzed using ANOVA. In the original models, I included sex, size, and interaction of sex by size as independent variables. If statistically nonsignificant, the interaction term was excluded from the final model. All statistical tests were two-tailed and tolerance for type I error was set at 0.05.

Determining the proportion of lobsters harvested in the fishery

To quantify exploitation level for female and male lobsters tagged within and outside of no-take reserves, I first determined the number of lobsters that were tagged each fall, in each area and sex category (e.g., fall 1997 Round Closed females), that were eligible for commercial harvest (i.e., number that were ≥82.5 mm CL (the minimum legal size) and were not ovigerous or V-notched; a V-notch is a shallow mark cut into the tail of an ovigerous female that is retained for up to two molts). The proportion harvested was considered to be the number of tagged lobsters from each category that were reported harvested during the spring, divided by the number from this category tagged the previous fall and eligible for commercial harvest.

One complicating factor was that the minimum legal size limit changed from 81 mm to 82.5 mm CL on 24 May 1998, 3 weeks after the harvesting season began and was maintained at the increased level for the rest of the study period. To simplify the analysis, I considered only lobsters that were ≥82.5 mm CL to be commercial sized. However, lobsters that were 81–82 mm CL may have been eligible for harvest during the first 3 weeks of the 1998 harvesting season. Any tagged lobsters that were <82.5 mm CL and harvested during this period were excluded from the analyses.

Results

Movement between zones

Among 890 lobsters that were marked and recaptured, 522 (58.7%) were recaptured in the same zone in which they were marked (i.e., they did not move). The remaining 368 (41.3%) individuals were recaptured in a different zone between 1 and 721 days after tagging. The proportion that moved was greater among lobsters recaptured during spring than during fall (Table 1), most likely a result of increased sampling outside of the immediate tagging area during spring. There were no significant differences in the frequency of lobsters that moved between Spring 1 and Spring 2 ($G_1 = 1.91$, $P = 0.17$) or between Fall 2 and Fall 3 ($G_1 = 0.88$, $P = 0.35$). Consequently, Spring 1 and Spring 2 were combined (hereafter referred to as Springs 1&2), as were Fall 2 and Fall 3 (referred to as Falls 2&3), for remaining analyses. Subsequently, I found significant differences in the frequency of lobsters that moved between Fall 1 and Falls 2&3 ($G_1 = 25.61$, $P < 0.0001$), between Fall 1 and Springs 1&2 ($G_1 = 172.80$, $P < 0.0001$), and between Falls 2&3 and Springs 1&2 ($G_1 = 42.31$, $P < 0.0001$), so none of these periods was pooled.

To assess if frequency of lobster movement was related to sex or size, I examined each area (Round Closed, Round Open, Duck Closed, and Duck Open) and sampling period (i.e., Fall 1, Falls 2&3, and Springs 1&2) separately. Initially, all models were run including an interaction term for sex by size, but in all cases, this interaction term was nonsignificant. Generally, proportions of lobsters that moved were similar for individuals of both sexes and sizes (Table 2). Further analysis indicated that the only significant difference in proportion of lobsters that moved in relation to sex occurred at Round Open – Falls 2&3 (females, 5/5 or 100.0% moved; males, 8/19 or 42.1% moved). Significant differences in relation to size occurred only at Round Closed – Falls 2&3 (sublegal-sized lobsters, 11/16 or 68.8% moved; commercial-sized lobsters, 20/61 or 32.8% moved) and Duck Closed – Fall 1 (sublegal-sized lobsters, 0/10 or 0.0% moved; commercial-sized lobsters, 14/64 or 21.9% moved; Table 2).

Distance traveled

During this study, no lobsters were observed to move between the Round Island and Duck Islands sites. The farthest distance traveled by any lobster was 4942 m (recaptured at Spring 1, after about 8 months at large). The distance moved was greater for individuals recaptured during spring than for individuals recaptured during fall (Fig. 4), likely a result of increased sampling outside of the immediate tagging area during spring. There was a significant difference in distance moved among recapture periods ($F_{4,363} = 22.73$, $P < 0.0001$). Further analysis indicated no significant differences between Spring 1 and Spring 2 (Fisher's PLSD; $P = 0.79$) or between Fall 2 and Fall 3 (Fisher's PLSD; $P = 0.64$). Consequently, Spring 1 and Spring 2 were combined, as were Fall 2 and Fall 3, for remaining analyses. Subsequently, I continued to find a significant difference among recapture periods ($F_{2,365} = 45.52$, $P < 0.0001$) and further analysis indicated no significant difference between Fall 1 and Falls 2&3 (Fisher's PLSD; $P = 0.47$), but significant differences were indicated between Fall 1 and Springs

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Table 1. Proportion of lobsters that moved between geographic zones and proportion of immigrants occurring within geographic areas (i.e., no-take reserves or nearby harvested areas) for 890 lobsters marked and recaptured.

	n	% moved between zones	% immigrants to area
Fall 1	326	17.2	1.5
Spring 1	311	64.0	11.9
Fall 2	166	35.5	9.0
Spring 2	53	73.6	34.0
Fall 3	34	44.1	5.9

Note: Recaptures occurred during five distinct periods: Fall 1 (1–13 days post-tagging), Spring 1 (209–282 days post-tagging), Fall 2 (324–379 days post-tagging), Spring 2 (580–644 days post-tagging), or Fall 3 (704–721 days post-tagging).

1&2 (Fisher's PLSD; $P < 0.0001$) and between Falls 2&3 and Springs 1&2 (Fisher's PLSD; $P < 0.0001$).

To assess if distance moved by lobsters was related to lobster sex or size, I examined each area (Round Closed, Round Open, Duck Closed, and Duck Open) and sampling period (i.e., Fall 1, Falls 2&3, and Springs 1&2) separately. Although I found no difference in mean distance moved by lobsters between Fall 1 and Falls 2&3, considering that the distance traveled by lobsters was much more likely to be limited by time during Fall 1 than during other recapture periods, I continued to separate these for the analysis. Generally, distance moved was similar for lobsters of both sexes and sizes (Fig. 5). No interaction term for sex by size was significant. There were no significant differences in distance moved between the sexes and the only significant difference in relation to size occurred at Round Open – Springs 1&2 ($F_{1,140} = 7.30$, $P = 0.008$).

Emigration from, and immigration to, no-take reserves

Among lobsters marked and recaptured, 813 (91.3%) were recaptured in the same area (no-take reserve or nearby harvested area) in which they were marked (i.e., they did not emigrate). The remaining 77 (8.7%) marked individuals were recaptured in the other area between 2 and 711 days after tagging. Initial examination of my data showed that the proportion of immigrants was greater during spring (particularly Spring 2) than during fall (Table 1). The proportion of immigrants between Fall 2 and Fall 3 was not statistically different ($G_1 = 0.39$, $P = 0.53$); however, there was a significant difference between Spring 1 and Spring 2 ($G_1 = 14.24$, $P = 0.0002$). This difference was due to an increased proportion of immigrants in nearby harvested areas during Spring 2 (e.g., Round Open – Spring 1, 12.6% immigrants; Round Open – Spring 2, 40.0% immigrants), likely a result of intense harvesting and a low exchange rate between reserves and nearby harvested areas rather than an increase in the frequency of emigration from reserves during this period. Despite this difference, I chose to pool Spring 1 and Spring 2, as well as Fall 2 and Fall 3, to increase sample size and to present results in a way consistent with the previous two sections. Subsequently, I found significant differences in the proportion of immigrants between Fall 1 and Falls 2&3 ($G_1 = 14.71$, $P = 0.0001$), between Fall 1 and Springs 1&2 ($G_1 = 46.89$, $P < 0.0001$), and between Falls 2&3 and Springs 1&2 ($G_1 = 5.36$, $P = 0.02$), so none of these time periods was pooled.

To assess if frequency of lobster emigration (or immigration) was related to lobster sex or size, I examined each area (Round Closed, Round Open, Duck Closed, and Duck Open) and sampling period (i.e., Fall 1, Falls 2&3, and Springs 1&2) separately. Generally, the frequency of immigrants was similar for lobsters of both sexes and sizes (Table 3). Initially, all models were run including an interaction term for sex by size, but in all cases, this interaction term was nonsignificant. Further analysis indicated that there were no significant differences in the proportion of immigrants in relation to sex and that the only significant difference in relation to size occurred at Duck Closed – Falls 2&3 (sublegal-sized lobsters, 3/18 or 16.7% immigrants; commercial-sized lobsters, 0/61 or 0.0% immigrants; Table 3).

Vulnerability to harvest

For all years, sites, and sexes, the proportion of lobsters harvested in the commercial fishery was significantly different for lobsters that were tagged outside of no-take reserves compared with those tagged inside reserves (Tables 4 and 5). Moreover, a much greater proportion of lobsters tagged were harvested at the Round Island site than at the Duck Islands site; this was true for lobsters tagged both within and outside of the reserve.

Generally, among lobsters eligible for commercial harvest, I found little evidence of a difference between females and males in their frequency of mortality related to fishery (Tables 4 and 5). However, there was a significant difference between female and male lobsters tagged at Round Open during fall 1997 and harvested during spring 1998.

Discussion

This study showed that most (522/890 or 58.7%) tagged lobsters were recaptured in the same zone in which they were marked (i.e., they did not move). In a previous study of lobsters near the Eastport Peninsula, Ennis et al. (1989) reported comparable results, indicating that 53% of lobsters recaptured after 335–395 days at large were in the immediate vicinity of where they were initially caught and tagged. Moreover, among lobsters that moved, the distances traveled over time were within a similar range between the two studies. Lobster movement patterns did result in exchange of lobsters between no-take reserves and nearby harvested areas. However, the amount of exchange was low (77/890 or 8.7% were immigrants) and more lobster exchange occurred at the Round Island site (67/603 or 11.1% were immigrants) than at Duck Islands (10/287 or 3.5% were immigrants).

My results corroborate other findings indicating that American lobster movement patterns in Newfoundland waters are restricted to small geographic areas (e.g., Ennis 1984*a*, 1984*b*; Ennis et al. 1989). Around the Eastport Peninsula, features of the coastal physiography and bottom topography may impede or restrict movement of lobsters. In this study, all minimum path distances extending from zones of origin to zones of termination resulted in movements oriented parallel to the coast and (or) maintaining the lobster in relatively shallow water (i.e., generally less than 20 m deep). Furthermore, no lobsters were observed to leave lobster

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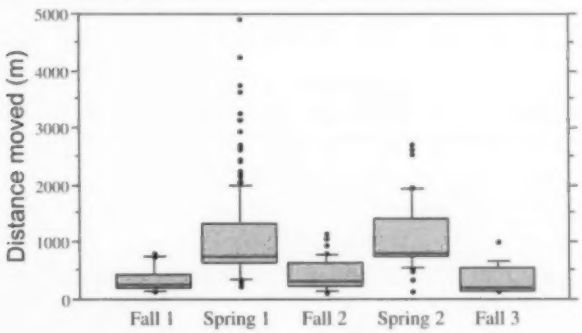
Table 2. Proportion of lobsters that moved between geographic zones in relation to sex and size for 890 lobsters marked and recaptured (separating different geographic areas of tagging and recapture periods).

	Female				Male							
	Sublegal		Commercial		Sublegal		Commercial		Sex		Size	
	n	% moved	*n*	% moved	*n*	% moved	*n*	% moved	χ^2_1	*P*	χ^2_1	*P*
Round Closed												
Fall 1	13	23.1	40	22.5	8	0.0	55	25.5	0.04	0.84	1.10	0.29
Falls 2&3	6	66.7	20	35.0	10	70.0	41	31.7	0.03	0.87	6.70	0.01
Springs 1&2	16	62.5	44	65.9	12	75.0	26	80.8	2.30	0.13	0.19	0.67
Round Open												
Fall 1	13	0.0	13	23.1	7	14.3	32	12.5	0.07	0.79	1.70	0.19
Falls 2&3	1	100.0	4	100.0	8	25.0	11	54.5	6.40	0.01	1.71	0.19
Springs 1&2	44	65.9	85	64.7	25	52.0	69	66.7	0.17	0.68	0.50	0.48
Duck Closed												
Fall 1	5	0.0	14	14.3	5	0.0	50	24.0	0.65	0.42	3.90	<0.05
Falls 2&3	6	33.3	21	23.8	9	22.2	40	35.0	0.36	0.55	0.10	0.75
Springs 1&2	0	—	3	100.0	0	—	3	100.0	—	—	—	—
Duck Open												
Fall 1	3	0.0	19	10.5	19	5.3	30	16.7	0.49	0.48	2.00	0.16
Falls 2&3	6	33.3	5	40.0	8	37.5	4	0.0	0.48	0.49	0.61	0.43
Springs 1&2	5	80.0	11	45.5	4	25.0	17	58.8	0.05	0.82	0.01	0.94

Note: Recapture periods: Fall 1 (1–13 days post-tagging), Fall 2&3 (324–379 or 704–721 days post-tagging), Spring 1&2 (209–282 or 580–644 days post-tagging). Data were analyzed using a generalized linear model with a binary response variable using a logit link function. Models first were run with an interaction term for sex by size, which was nonsignificant in all cases and removed from final models.

Fig. 4. Variation in distance moved among 368 lobsters marked and recaptured in a different geographic zone from the one in which tagged. Recaptures occurred during five distinct periods: Fall 1 (1–13 days post-tagging; $n = 56$), Spring 1 (209–282 days post-tagging; $n = 199$), Fall 2 (324–379 days post-tagging; $n = 59$), Spring 2 (580–644 days post-tagging; $n = 39$), or Fall 3 (704–721 days post-tagging; $n = 15$). Box plots indicate 10th percentile (lower bar), 25th percentile (bottom of box), median (black line through box), 75th percentile (top of box), and 90th percentile (upper bar); outliers are represented by points.



grounds surrounded by deep water. It is possible that lobster movement was inhibited by excessively deep water or the presence of seasonal thermoclines (see Ennis 1984*b*). The influence of physical environmental features on lobster movement patterns should be considered when selecting areas for reserve establishment.

Generally, I derived indices of lobster movement that showed higher values during spring than during fall but this was more likely due to the sampling design than any actual difference among seasons. During spring, commercial harvesting (and hence sampling) intensely occurred over a large geographic area, whereas during fall, my sampling effort was less intense and restricted to a relatively small geographic area. Consequently, the spring sample was likely to have contained a greater proportion of individuals that left the general tagging area and thus moved from their zone of origin, possibly having traveled farther distances than those that remained within the general tagging area. There was no evidence for a relationship between time at large and lobster movement, and other studies of lobsters in coastal areas also failed to find such relationships (e.g., Ennis et al. 1989, 1994; Comeau et al. 1998).

I found a significant difference between Spring 1 and Spring 2 in the proportion of immigrants. This difference was due to a high proportion of immigrants in nearby harvested areas during Spring 2. Because I found no difference in the proportion of lobsters that moved or in distance traveled among lobsters that moved between Spring 1 and Spring 2, I do not believe that emigration from reserves increased during this period. In this study, only lobsters tagged during fall 1997 would have had an opportunity to be recaptured 580–644 days post-tagging (Spring 2). Because most lobsters tagged and recaptured remained in their zones of origin and local harvesting pressure was intense, lobsters tagged in harvested areas during fall 1997 were likely to remain there and die upon capture during the following commercial fishery (Spring 1). Consequently, there would have been few lobsters tagged in harvested areas during fall 1997 available for recapture during Spring 2, and any lobsters tagged in reserves during fall 1997 that spilled over to harvested areas after Spring 1 would represent a large proportion of the 1997 tagged lobsters present there (thus causing the proportion of immigrants to the area to appear high even though emigration from the reserves may not have increased). Similarly, because movement rates were low and

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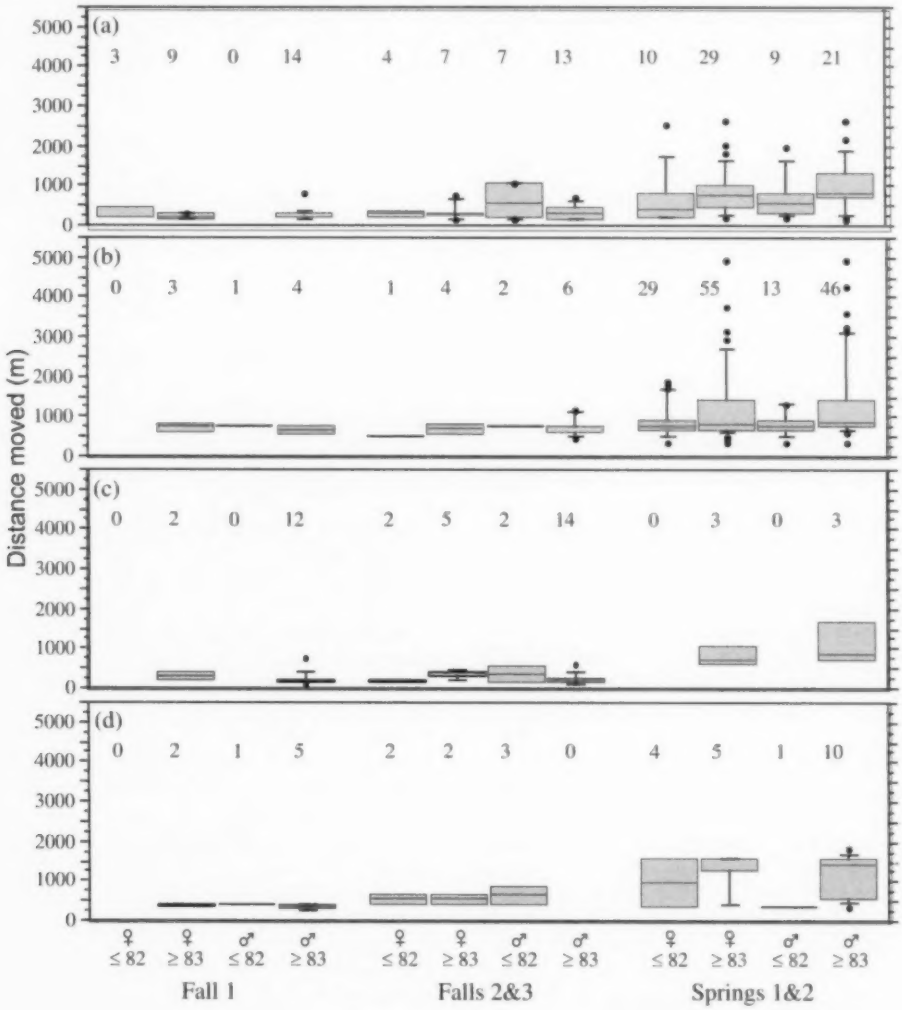
Fig. 5. Variation in distance moved in relation to sex and size among 368 lobsters marked and recaptured in a different geographic zone from the one in which tagged (separating different geographic areas of tagging and recapture periods). Geographic areas of tagging: (*a*) Round Closed, (*b*) Round Open, (*c*) Duck Closed, and (*d*) Duck Open. Recapture periods: Fall 1 (1–13 days post-tagging), Fall 2&3 (324–379 or 704–721 days post-tagging), Spring 1&2 (209–282 or 580–644 days post-tagging). Box plots indicate 10th percentile (lower bar), 25th percentile (bottom of box), median (black line through box), 75th percentile (top of box), and 90th percentile (upper bar); outliers are represented by points. Sample sizes are given above estimates.



most lobsters eligible for harvest were removed from harvested areas during the fishery, the proportion of immigrants in these areas was generally lower during Falls 2&3 (after the harvest and before much emigration from reserves had occurred) than during Spring 1&2 (after several months had passed and more new immigrants had an opportunity to arrive).

In general, there did not seem to be a relationship between lobster movement patterns and lobster sex or size. However, at Round Open during Falls 2&3, I found that more females than males moved to a new zone between tagging and recapture. In addition, I found three cases in which there were differences in movement patterns in relation to lobster size: (*i*) more sublegal- than commercial-sized lobsters moved to a new zone between tagging at Round Closed and recapture during Falls 2&3; (*ii*) commercial-sized lobsters tagged at Round Open and recaptured during Springs 1&2 moved farther than sublegal-sized individuals; and (*iii*) more sublegal- than commercial-sized lobsters were immigrants to Duck Closed during Falls 2&3. These results were somewhat difficult to interpret. Unfortunately, this is a rather common theme among studies of lobster movement patterns in coastal areas: other studies have generally found little variation in movement parameters in relation to sex or size but most also reported a few anomalous results that did not fit this pattern (e.g., Ennis et al. 1989, 1994; Comeau et al. 1998). Moreover, comparison of such anomalous results among studies also has shown few general trends; I believe

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Table 3. Proportion of immigrants occurring within geographic areas (i.e., no-take reserves or nearby harvested areas) in relation to sex and size for 890 lobsters marked and recaptured (separating different geographic areas of recapture and recapture periods).

	Female				Male							
	Sublegal		Commercial		Sublegal		Commercial		Sex		Size	
	n	% immigrant	*n*	% immigrant	*n*	% immigrant	*n*	% immigrant	χ^2_1	*P*	χ^2_1	*P*
Round Closed												
Fall 1	13	0.0	41	2.4	8	0.0	56	3.6	0.10	0.75	1.10	0.29
Falls 2&3	6	0.0	22	13.6	8	12.5	43	9.3	0.02	0.87	0.19	0.66
Springs 1&2	13	7.7	29	6.9	8	12.5	9	11.1	0.29	0.59	0.02	0.90
Round Open												
Fall 1	13	0.0	12	0.0	7	0.0	31	3.2	0.66	0.42	0.41	0.52
Falls 2&3	1	0.0	2	50.0	10	30.0	9	22.2	0.06	0.80	0.00	0.97
Springs 1&2	47	8.5	100	17.0	29	17.2	86	20.9	1.27	0.26	1.76	0.18
Duck Closed												
Fall 1	5	0.0	14	0.0	5	0.0	51	2.0	0.49	0.48	0.19	0.66
Falls 2&3	7	14.3	21	0.0	11	18.2	40	0.0	0.05	0.83	9.33	0.002
Springs 1&2	0	—	0	—	0	—	0	—	—	—	—	—
Duck Open												
Fall 1	3	0.0	19	0.0	19	0.0	29	0.0	—	—	—	—
Falls 2&3	5	0.0	5	0.0	6	0.0	4	0.0	—	—	—	—
Springs 1&2	5	0.0	14	21.4	4	0.0	20	15.0	—	—	—	—

Note: Recapture periods: Fall 1 (1–13 days post-tagging), Fall 2&3 (324–379 or 704–721 days post-tagging), Spring 1&2 (209–282 or 580–644 days post-tagging). Data were analyzed using a generalized linear model with a binary response variable using a logit link function. Models first were run with an interaction term for sex by size, which was nonsignificant in all cases and was removed from final models.

Table 4. Number of female and male lobsters tagged within no-take reserves and nearby harvested areas during fall eligible for commercial harvest (i.e., ≥82.5 mm carapace length, not ovigerous or V-notched) and proportion reported harvested during following spring commercial lobstering season.

	No-take reserve				Harvested area			
	Females		Males		Females		Males	
	n	% harvested	*n*	% harvested	*n*	% harvested	*n*	% harvested
Round Island								
Fall 1997 – spring 1998	27	18.5	101	12.9	57	71.9	76	52.6
Fall 1998 – spring 1999	45	6.7	67	6.0	49	65.3	54	48.1
Duck Islands								
Fall 1997 – spring 1998	28	3.6	66	1.5	16	31.3	26	11.5
Fall 1998 – spring 1999	35	0.0	78	2.6	26	30.8	44	40.9

Table 5. *G* test results for comparisons of proportions of lobsters harvested during spring commercial harvesting between lobsters tagged within and outside of no-take lobster reserves (separating sexes) and between tagged females and males (separating locations of tagging: within and outside of no-take lobster reserves) at Round Island and Duck Islands sites during fall of previous year.

	No-take reserve versus harvested area				Females versus males			
	Females		Males		No-take reserve		Harvested area	
	G_1	*P*	G_1	*P*	G_1	*P*	G_1	*P*
Round Island								
Fall 1997 – spring 1998	22.14	<0.0001	33.37	<0.0001	0.53	0.47	5.18	0.02
Fall 1998 – spring 1999	38.81	<0.0001	30.44	<0.0001	0.02	0.88	3.10	0.08
Duck Islands								
Fall 1997 – spring 1998	6.55	0.01	3.95	<0.05	0.37	0.55	2.43	0.12
Fall 1998 – spring 1999	—	0.0005[a]	30.72	<0.0001	—	1.00[a]	0.73	0.39

[a] *P* calculated using Fisher's exact test because one cell contained a value of 0.

there may be no biological significance to these statistical anomalies.

My results suggested that local exploitation rate of lobsters was quite high, up to 71.9% for some population components. Furthermore, because overwinter streamer tag loss has been shown to be substantial (17.8% of lobsters lose their streamer tags during the overwinter period; Rowe and Haedrich 2001), the proportions of lobsters harvested should

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be corrected to account for such loss, thus causing estimates of local exploitation rate to be even higher. Although, Karnofsky and Price (1989) found that some lobsters never enter into traps. Consequently, because all lobsters tagged in my study were initially captured using traps, my estimates of exploitation rate may have actually applied to trap-prone lobsters only rather than to the whole population; therefore, my estimates of exploitation rate may have been high. However, I found that many more lobsters tagged in nearby harvested areas were harvested than lobsters that were tagged in no-take reserves, likely a result of low frequency of movement between these two areas. In addition, comparison of the frequency of mortality between the Duck Islands site and Round Island suggested that exploitation rates were much lower in the general area of the Duck Islands, probably a result of both higher exposure and poor weather conditions during spring, which often deterred harvesting in this area.

Relative to males, female lobsters may be offered some additional protection from the fishery by the presence of eggs and (or) a V-notch. Release of ovigerous females is one of the oldest conservation measures for lobsters and serves to preserve existing clutches of eggs to hatching (Miller 1995). However, because female lobsters typically bear eggs only every second year (Waddy et al. 1995), unless coupled with V-notching, this measure only protects mature females while ovigerous. When V-notched animals are recaptured later, after having released their eggs, they are returned to the water and this measure has the effect of protecting known spawners for several additional years. Under current regulations in Newfoundland, V-notching by harvesters is voluntary but landing of V-notched animals is prohibited. Because of increased protection offered to females, harvesting could result in altered sex ratios. However, I found some evidence to suggest that among individuals eligible for commercial harvest, the frequency of mortality related to the fishery can be higher for females than males (i.e., lobsters tagged at Round Open during fall 1997 and harvested during spring 1998). Even though females receive additional protection, their increased catchability may result in similar exploitation rates for both sexes.

Differences between Bonavista Bay lobster populations in no-take reserves and nearby harvested areas during the first 3 years of reserve status (1997–1999) have been reported (Rowe 2001), although the response of lobsters to protection has been variable both between sites and sexes. At the Round Island site, lobsters seemed to have responded well to local protection: within the reserve, average female and male size increased over time, as did the proportion of ovigerous female lobsters. However, at the Duck Islands reserve, the response was different: male size increased over time, but there was no change in average female size or the proportion of ovigerous females. Spatial comparisons at the Round Island site indicated that population density was higher, and females and males were larger, within the reserve than in the nearby harvested area. In addition, within the Round Island reserve, a greater proportion of females were ovigerous. Spatial comparisons between the reserve and nearby harvested area at the Duck Islands site indicated that population densities in the two areas were similar. Also, although females and males were larger within the reserve relative to outside, there was no difference in the proportion of females that were ovigerous between the two areas. Taken together, these data were consistent with the notion that no-take reserves improved lobster populations within them, particularly at the Round Island site.

An explanation of observed differences among lobster population parameters in small no-take reserves is provided by this study. Because the frequency of lobster emigration from reserves was relatively low and harvesting pressure outside of reserves was intense (annual harvesting mortality amounted up to 71.9% for lobsters eligible for harvest), protection from exploitation resulted in higher mean lobster sizes within reserves. Although movement between the reserve and nearby harvested area was less frequent at the Duck Islands site, differences in population parameters between these areas were less pronounced relative to the Round Island site. This may have been due to the relatively low levels of exploitation that occurred in the Duck Islands area (annual harvesting mortality for lobsters eligible for harvest and tagged in the harvested area was 11.5–40.9% and 48.1–71.9% at the Duck Islands and Round Island sites, respectively). If exploitation rates measured in this area during 1998 and 1999 reflected a general pattern for the site, then it is probable that the lobster population at the Duck Islands was in a more pristine state at the onset of reserve establishment. If so, because older–larger lobsters molt less frequently (Waddy et al. 1995), increases in mean lobster size will be slower to appear, and with an alternate-year reproductive cycle (Waddy et al. 1995), the proportions of females that were ovigerous may also have been approaching an upper limit.

Although these no-take reserves have only been established for a few years, my results indicate that they offer increased survival to lobsters within them and therefore have the potential to provide direct benefits to the local lobster population and fishery. This may happen in two ways: through elevated egg production by individuals within the reserves and (or) by movement of juvenile or adult lobsters from reserves to harvested areas (Roberts and Polunin 1991; Rowley 1994). Fecundity of American lobsters increases exponentially with increasing female size (Ennis 1981). Because of greater mean size of female lobsters within no-take reserves (Rowe 2001), their egg production would be greater relative to those from nearby harvested areas. However, considering that only 1.5% of lobsters within the Eastport Peninsula Lobster Management Area receive protection within no-take reserves (Rowe 2001), the supplement to total local egg production from the two reserves described here may be small, although even a modest contribution could be vital in view of extremely low levels of egg production that currently predominate (FRCC 1995). To further augment local egg production, a larger proportion of the area should be closed to harvesting. Because these lobsters appear to have small home ranges, this measure may reduce the frequency of emigration from reserves and provide more protection to individuals from exploitation. Other measures such as a reduction in harvesting effort, an increase in minimum carapace size, and extensive V-notching could have similar effects on population egg production and may be used in conjunction with, or as alternatives to, no-take reserves. Further research is needed to quantify the relative merits of various management options.

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The local fishery may be enhanced by movement of juvenile or adult lobsters from no-take reserves to nearby harvested areas. If this is to happen, emigration from no-take reserves must be greater than immigration to no-take reserves and must also offset the removal from exploitation of protected populations (Roberts and Polunin 1991; Rowley 1994). In this study, more tagged lobsters emigrated from no-take reserves than immigrated to these areas (Round Closed, 16/256 or 6.3% were immigrants; Round Open, 51/347 or 14.7% were immigrants; Duck Closed, 4/154 or 2.6% were immigrants; Duck Open, 6/133 or 4.5% were immigrants). In addition, tagged lobsters that emigrated from reserves and were harvested were generally much larger than most other lobsters taken. If no-take reserves are sanctioned based on gains to fisheries, it will be critical to quantify if movement of adult lobsters from reserves to harvested areas improves the local fishery enough to compensate for removal from exploitation of the protected population.

My preliminary study of these no-take lobster reserves suggests that they may be useful conservation tools, although response of lobsters in different areas to reserve protection will likely depend on size of the reserve in relation to the extent of local lobster movement and local exploitation rates in nearby harvested areas. In Newfoundland waters, lobsters are heavily exploited and individuals appear to move very little (e.g., Ennis 1984*a*, 1984*b*; Ennis et al. 1989). Consequently, even small no-take reserves may be effective. However, some American lobster populations undertake extensive inshore–offshore migrations and commonly disperse long distances (e.g., Cooper and Uzmann 1971; Campbell 1986; Pezzack and Duggan 1986), and with those populations, reserves would have to be relatively large to show similar results.

Acknowledgements

The author is grateful for the kindness extended to her by harvesters of the Eastport Peninsula Lobster Protection Committee and their families; this research would not have been possible without their assistance. The author also thanks Kelly Barrington, Ray Elliott, Rick Elliott, Gerald Ennis, George Feltham, Leanne Hancock, Catherine Hood, Gordon Janes, Lee Janes, Ian Jones, John Lawson, Niall O'Dea, Craig Penney, Ted Potter, Harry Rowe, Boyd Squire, and Wade Turner for assisting with data collection. Richard Haedrich supervised the M.Sc. thesis work of which this paper is a part, and he is thanked for his guidance. Gerald Ennis, Glen Jamieson, Ian Jones, Jon Lien, Greg Robertson, Paul Snelgrove, Robert Steneck, and one anonymous referee reviewed an earlier version of this manuscript and offered many helpful comments. This research was made possible by financial support from the Natural Sciences and Engineering Research Council, the Canadian Centre for Fisheries Innovation, and the Department of Fisheries and Oceans Canada, as well as in-kind support provided by Memorial University and Parks Canada.

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Sulfur burial in and loss from the sediments of Little Rock Lake, Wisconsin

N.R. Urban and A.E. Monte

Abstract: Lake sediments often are regarded as accurate records of changes in climatic conditions, rates of atmospheric deposition of substances to the lake, or other processes occurring within lakes. In this study, the sedimentary record of sulfur was examined in Little Rock Lake, Wisconsin. This lake received experimental sulfate additions from 1985 through 1990, and a mass balance showed that 35% (425 kg) of experimental sulfur additions were buried in the sediments. Sediment cores collected before and after sulfur additions confirmed that burial of 180–360 kg of sulfur occurred during the 6 years of experimental sulfur additions. However, cores collected in 1992 and 1996 contained less sulfur than cores taken in 1990 and suggested that sulfur incorporation in sediments is not permanent. To examine seasonal sulfur loss from sediments, sulfur inventories in the top 4 cm of sediments were measured in multiple cores before and after fall overturn. At water depths greater than 5 m, surface sediments retrieved after fall overturn had significantly less sulfur than did those collected before overturn. The small seasonal release from the sediments (25 kg S in 1996) might be caused by organic matter decomposition or sulfide oxidation.

Résumé : Les sédiments lacustres sont souvent considérés comme des témoins fidèles des changements dans les conditions climatiques, dans les taux de précipitation atmosphérique de substances et dans plusieurs autres processus en opération dans les lacs. Notre étude examine la présence du soufre dans les sédiments du lac Little Rock, au Wisconsin. Ce lac a reçu des apports expérimentaux de sulfates de 1985 à 1990 et un bilan massique montre que 35% (425 kg) du soufre ajouté est enfoui dans les sédiments. Une comparaison de carottes de sédiments récoltées avant et après l'ajout de soufre confirme l'enfouissement de 180–360 kg de soufre durant les 6 ans de l'expérience. Cependant, des carottes récoltées en 1992 et en 1996 contiennent moins de soufre que celles prises en 1990, ce qui laisse croire que l'incorporation du soufre dans les sédiments n'est pas permanente. Des mesures du soufre dans les 4 cm supérieurs des sédiments dans un grand nombre de carottes avant et après le brassage d'automne ont permis d'évaluer la perte saisonnière de soufre des sédiments. Aux profondeurs supérieures à 5 m, les sédiments superficiels contiennent significativement moins de soufre après le brassage d'automne qu'avant. La faible libération saisonnière de soufre par les sédiments (25 kg S en 1966) est peut-être le résultat de la décomposition de la matière organique ou de l'oxydation des sulfures.

[Traduit par la Rédaction]

Introduction

Sulfur enters lake sediments by either diffusion of sulfate (or other dissolved species) from the overlying lake water or deposition of seston. The diffusive influx of sulfate is driven by a concentration gradient induced by microbial reduction of sulfate to sulfide within the sediments. The hydrogen sulfide that is produced may either diffuse back into the water column or react to form solid phases (e.g., FeS, elemental sulfur, organic sulfur compounds; Berner 1984; Nriagu and Soon 1985; Rudd et al. 1986). The sulfur in seston is in various chemical forms including SO_4^{2-}, organic sulfate esters, and a variety of organic compounds containing reduced sulfur (i.e., (II-) oxidation state; David and Mitchell 1985). Decomposition of organic matter in sediments releases sulfur as hydrogen sulfide that, as above, may either react in the sediments or diffuse into the lake. The question addressed in this paper is what fraction of the sulfur entering the sediments remains fixed in solid forms and what fraction returns to the water column?

The release of sulfur from sediments is of interest for a couple of reasons. First, fixation of sulfur by any means in lake sediments results in a generation of alkalinity (e.g., Schindler 1986; Anderson and Schiff 1987; Urban and Baker 1989) that can counteract the atmospheric deposition of acids. A release of sulfur from lake sediments will, in contrast, generate acidity and thus negate the alkalinity initially gained from incorporation of S into the sediments. For softwater lakes with long water residence times, sulfate diffusion into sediments and subsequent reduction is thought to represent a significant source of alkalinity that can protect these lakes from acidification (Schindler 1986; Schindler et al. 1986). This hypothesis is incorrect if the sulfur is not permanently stored in the sediments.

Second, sulfur fixation in sediments has been thought to regulate the bioavailability and hence toxicity of trace metals (DiToro et al. 1990; cf. Lee et al. 2000). Because many metal sulfides are only sparingly soluble, the presence of hy-

Received August 4, 2000. Accepted March 23, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 4, 2001.
J15899

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 DOI: 10.1139/cjfas-58-7-1347 © 2001 NRC Canada

drogen sulfide causes precipitation of the metal sulfides. However, it has been suggested that metal sulfides are oxidized and released from the sediments during periods of lake overturn (Kling et al. 1991). Clearly, such oxidation of sulfides would render the trace metals once more bioavailable and toxic.

Stratigraphy in lake sediments has been used to reconstruct past conditions. Increases in total sulfur content of sediments have been interpreted as a record of increasing rates of acid deposition (e.g., Mitchell et al. 1985). Sulfide-rich sapropels have been interpreted as records of periods of anoxia in bottom waters (Zaback and Pratt 1992; Henneke et al. 1997). The profiles of C, N, P, and S in sediments have been used to deduce rates of early diagenesis (e.g., Berner 1980; Billen 1982; Wang and Van Cappellen 1996). There has been considerable discussion in recent literature about reduced sulfur masking the paleorecord by reacting with organic biomarkers (e.g., Kohnen et al. 1991). To accurately interpret the sediment record, however, we need to understand the factors controlling release of sulfur from the sediments.

The study described here entailed an examination of the sediments of Little Rock Lake, a lake that received artificial additions of sulfuric acid to the water column for 6 years. Acid additions increased the sulfate concentration in the water column from an initial value of 28 μM to 80 μM and caused a drop in pH from 6.1 to 4.7. The increased sulfate inventory in the water column accounted for only 50% of the total amount (1175 kg S) of sulfate experimentally added to the lake (Urban et al. 2001). In the lake-acidification experiment in the Experimental Lakes Area (ELA), it similarly was reported that the acid additions were only 31–38% efficient in lowering the pH (Schindler et al. 1980). The remaining 50% of the sulfur added to Little Rock Lake was lost from the water column via several processes including (*i*) outseepage, (*ii*) algal uptake of sulfur and burial of seston, and (*iii*) sulfate reduction followed by fixation of reduced sulfur in the sediments. The latter two mechanisms do not necessarily represent permanent removal of sulfate from the lake water; recycling of S from sediments to the lake water has been reported previously (Rudd et al. 1986; Kling et al. 1991). The objectives of this study were to quantify the relative magnitudes of the three loss mechanisms and to determine if and how quickly sulfur is recycled from the sediments back to the lake water.

Methods

Site description

Little Rock Lake is an oligotrophic, softwater, seepage lake in northern Wisconsin (45°59′N, 89°42′W). The lake has a natural constriction that divides it into two distinct basins (termed north and south). The total surface area of the lake is 18.2 ha, and the maximum depth is 10.5 m in the north basin and 6.5 m in the south basin. The lake is dimictic, but only the north basin stratifies in summer and becomes anoxic in the hypolimnion. The shallow south basin remains well mixed in summer.

Little Rock Lake was the site of an artificial acidification experiment (Brezonik et al. 1986, 1990, 1993). In 1984, a reinforced polyvinyl curtain was installed at the natural constriction to separate the two basins (Fig. 1). The north basin was acidified with sulfuric acid from 1985 through 1990, and the south basin was used as a control. The acidification increased the sulfate concentration in the north basin from an initial concentration of 27 μM to about 80 μM and lowered the pH from 6.1 to 4.7. No additional sulfuric acid has been added since 1991; the dividing curtain has been left in place, but otherwise the lake has been allowed to "recover" without intervention.

Sampling

Sediment cores were retrieved from the same location in the north basin (5 m depth) in 1985, 1990, 1992, and 1996 (Fig. 1), and cores also were collected at 7- and 9-m sites in 1985 and 1996. The analyses of the cores taken in 1985 have been published previously (Baker et al. 1992). Gravity cores taken in 1990 and 1992 were extruded, sliced into 2-cm increments, and kept frozen until they were analyzed for total sulfur in 1997. The gravity cores (4-cm diameter, 40- to 60-cm length) taken in 1996 were capped and refrigerated for transport to the laboratory where they were extruded and sectioned (1-cm increments to 20-cm depth, 2.5-cm increments between 20 and 40 cm, and 5-cm increments below 40 cm). Half of each depth section was placed into a Whirl-Pak® bag containing 3 mL of 20% Zn acetate solution. The other half was placed into a separate Whirl-Pak® bag. Both sections were then frozen.

To examine the seasonal release of sulfur from the sediments, short sediment cores were taken at multiple locations in both basins in August 1996 and again at the same locations in January 1997 (Fig. 1). A gravity corer was used to obtain 4 cm of surface sediments at 13 sites in the north basin and at 11 sites in the south basin. The sites in both basins lay along two intersecting transects spanning the length and width of the basins. The top 4 cm of each core was extruded at the site, placed in plastic bottles containing 3 mL of 20% zinc acetate solution, and stored in a cooler (<12 h) until they could be frozen.

Water samples were collected twice a month to examine seasonal and long-term trends of sulfate. Samples were collected at the deepest sites in each basin. On one of the two monthly sampling dates, samples were taken at 0.5-m intervals over the full depth of the water column using a peristaltic pump with Tygon® tubing. The other monthly samples, taken by the Trout Lake Research Center, were collected at 2-m increments. The 30-mL samples were filtered (0.45 μm Nuclepore polycarbonate filters), refrigerated, and returned to the lab for measurement of sulfate and chloride.

Analysis

The sediments cores collected in 1985 and 1996 were analyzed for inorganic and total sulfur. Inorganic sulfur was measured with the chromium-reduction technique (CRS) of Zhabina and Volkov (1978). Samples frozen with zinc acetate were used for this analysis. The liberated sulfide was measured after reaction with I_2 by titration with thiosulfate. For the CRS analyses, precision was 10–15%, recovery of standard (ZnS) spikes averaged 95%, and blanks were undetectable. Total sulfur and carbon were measured on freeze-dried samples with a Fisons Instruments elemental (CHNS) analyzer. Precision for the total S and C averaged 4% and 2%, respectively. Analysis of Round-Robin standards yielded values 98% and 104% of the means for S and C, respectively. Cores collected in 1990 and 1992 also were freeze-dried and analyzed with the CHNS analyzer. Although Amaral et al. (1989) reported that drying of sediments by any means causes a loss of S (both organic and inorganic forms), because the analytical technique was identical for all cores reported here, loss of S by drying could not explain systematic differences among cores.

Water samples were analyzed for temperature and concentrations of dissolved oxygen, sulfate, and chloride. Temperature and dissolved oxygen concentration were measured (YSI DO meter

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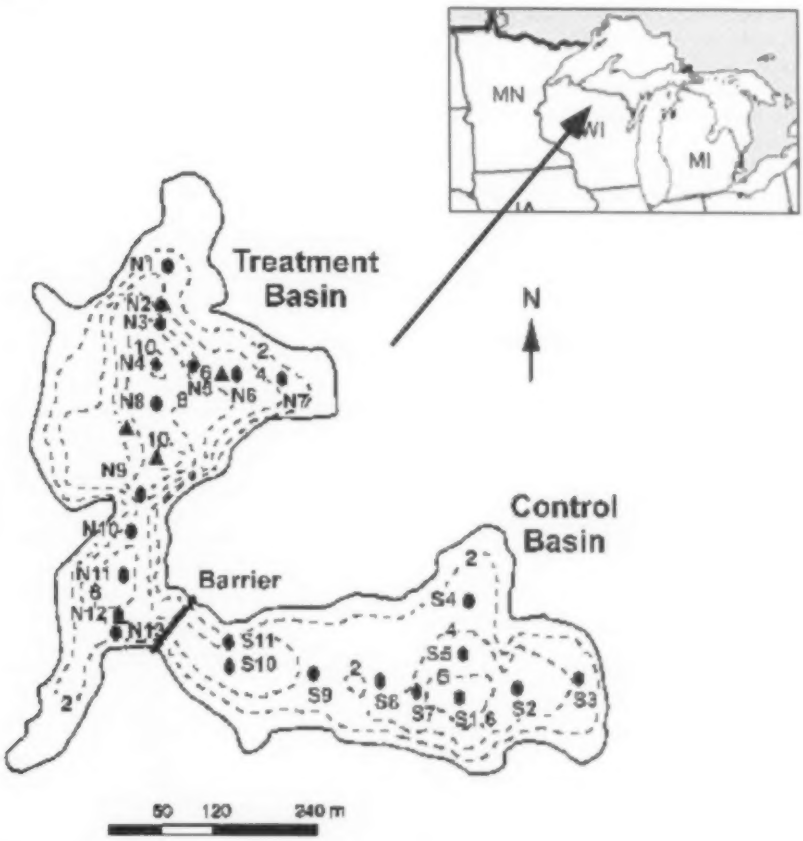
Fig. 1. Map of Little Rock Lake, Wisconsin, U.S.A., showing coring locations (45°59′N, 89°42′W). Triangles indicate locations of sediment cores retrieved in 1996; the site at 5-m depth was the same for cores retrieved in 1985, 1990, 1992, and 1996. Circles marked N1–N13 and S1–S11 indicate sites where surface sediments (0–4 cm) were sampled before and after fall overturn. Depth contours are in 2-m intervals.



model 58 and probe model 5730) at the lake. The filtered samples were analyzed for sulfate and chloride with a Dionex Ion Chromatograph (Dx-500). Precision for sulfate was 3% and 6% for chloride in replicate lake water samples. Detection limits (three × standard deviation, SD) were 7 μM for sulfate and 2 μM for chloride. Analysis of certified standards (Simulated Rainwater SRM 2694a-I, 2694a-II, National Institute of Standards and Technology, NIST) yielded values of 99.7% and 96.0% of the certified value for sulfate and 99.4% and 78.1% for chloride.

Sediment chronology

This study uses the sediment chronology published by Baker et al. (1992) and amplified in Engstrom et al. (1994). The sediment cores retrieved in 1985 were assayed for unsupported ^{210}Pb, and dates for these cores were calculated with the constant rate of supply (CRS) model. The ^{210}Pb-based dates agreed well with measured pollen horizons (Baker et al. 1992), and the inventories of ^{210}Pb in the sediments (12.5–21.7 pCi·cm^{-2}) were consistent with an atmospheric deposition rate of 0.46 pCi·cm^{-2}·year^{-1} (Urban et al. 1990), enhanced by sediment focusing to deep locations of the lake (Engstrom et al. 1994; Urban et al. 2001). Sediment cores retrieved at the same 5-m location (triangulation from shoreline markers) in the north basin in 1985, 1990, 1992, and 1996 were used for a detailed historical comparison. The ^{210}Pb profile in the 1985 core (Fig. 2; Baker et al. 1992) indicated that the sedimentation rate at this site has been relatively constant for the past 100 years, and hence the later cores were not assayed for ^{210}Pb.

Fig. 2. Historical changes in S inventories (concentrations) in the north basin of Little Rock Lake. Acid additions to the north basin increased the inventory more than threefold above its initial values. After cessation of acid additions in 1990, S inventories have declined as a result of flushing of the lake and burial of S in sediments. ◆, north basin; □, south basin.

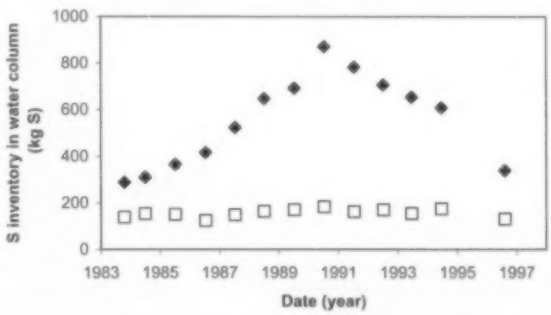


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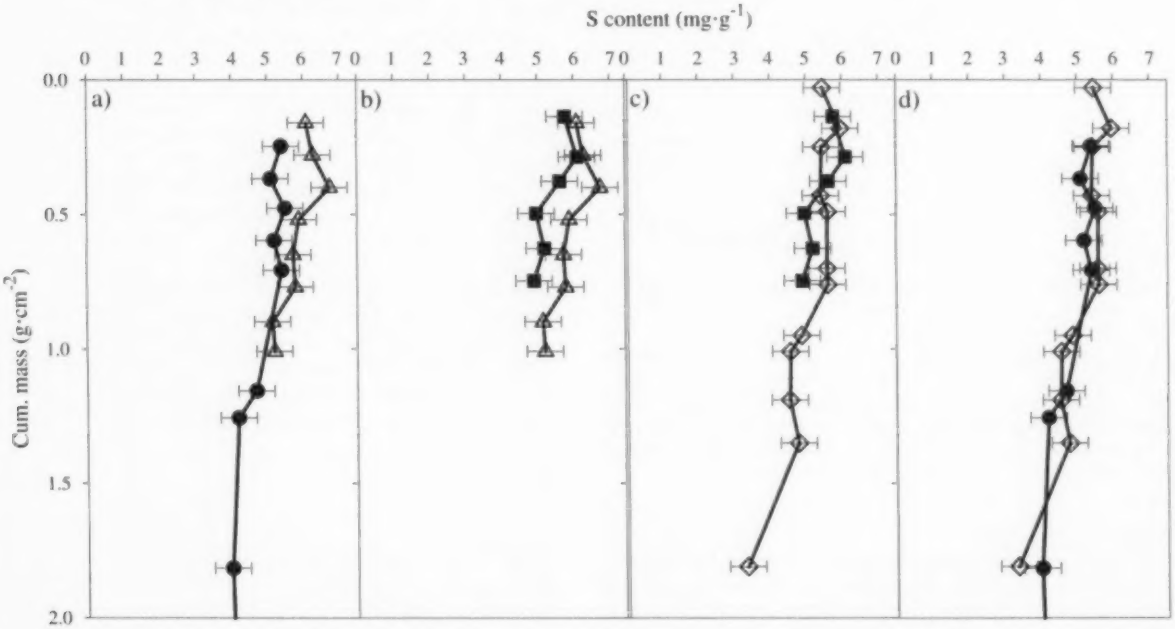
Table 1. Sulfur mass balance (kg) for the north basin of Little Rock Lake (data from Urban et al. 2001).

	Periods[a]						
	1985–1986	1986–1987	1987–1988	1988–1989	1989–1990	1990–1991	Cumulative[b]
Inputs[c]	66	53	59	47	44	50	
Acid addition	214	86	237	142	287	209	1175 (100)
Outseepage	51	56	79	63	63	49	362
Excess outseepage[d]	10	23	38	33	39	33	275 (15)
Change in storage[e]	66	125	70	58	151	106	576 (49)
Burial in sediments[f]	163	–43	147	68	117	104	(36)

[a]Periods are water years from 1 October to 30 September.
[b]The cumulative fluxes for the 6 years are reported in kilograms for acid additions, outseepage, and change in storage. The numbers in parentheses represent the cumulative flux as a percentage of the total acid addition.
[c]Inputs include wet and dry atmospheric deposition, leaf litterfall, and transfer from the south basin of the lake.
[d]Excess outseepage is an estimate of the increase in outseepage caused by sulfate additions to the lake. Excess outseepage for any year i is calculated as total outseepage for year i × (1 minus the ratio of the sulfate concentration in the north basin before acid additions to the sulfate concentration in year i).
[e]Change in storage is calculated as the difference in sulfate inventories in the lake (lake volume × lake sulfate concentration) at the beginning and end of the year.
[f]Burial in sediments is calculated by difference as inputs + acid additions – outseepage – change in storage.

Fig. 3. Sulfur profiles in sediment cores collected at 5-m water depth in the north basin of Little Rock Lake. The vertical axis (cumulative mass) is proportional to age; the horizon corresponding to 1940 is at 0.65 g·cm^{-2}. Comparison of cores taken in (*a*) 1985 (●) and 1990 (△), (*b*) 1990 (△) and 1992 (■), (*c*) 1992 (■) and 1996 (◇), and (*d*) 1996 (◇) and 1985 (●) suggests that sulfur buried as a result of the acid additions was slowly lost from the sediments following cessation of acid additions. Cores taken before 1996 are shown beginning at depths corresponding to the amount of sediment that would have accumulated in the years between 1996 and the time at which the core was taken. Error bars represent 95% confidence intervals and incorporate both analytical uncertainty and spatial variability observed at 5-m depth in the lake.



Results and discussion

Relative rates of outseepage, seston burial, and microbial sulfate reduction

Little Rock Lake is perched above the regional groundwater table, and outseepage is a major component of the hydrologic and solute budgets (e.g., Rose 1993; Sampson 1999; Urban et al. 2001). The flux of water seeping from the north basin of the lake to the water table was calculated previously from measured piezometric heads and hydraulic conductivities of the lake sediments (Rose 1993), and the sulfate flux has been assumed to be this water flux × the concentration of sulfate in the surface water of the lake (Urban et al. 2001). The amount of sulfur estimated in this manner to have been lost via outseepage (360 kg) during the 6 years of acid additions is 31% of the total amount experi-

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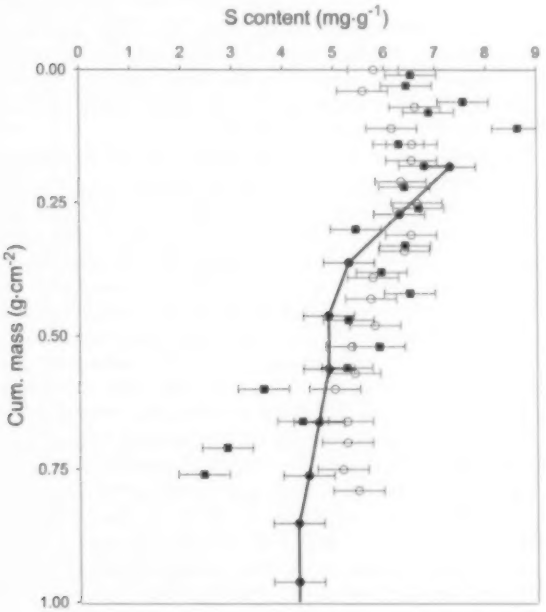
Fig. 4. Sulfur profiles in replicate cores collected at 7-m water depth in the north basin of Little Rock Lake. At cumulative (cum.) sediment masses less than 0.5 g·cm^{-2} (~1942), the concentrations in the two replicate cores are not significantly different from one another (Student's *t* test) or (with the exception of one point) from concentrations measured in the 7-m core taken in 1985, even though this core was taken from a different location in the lake. The sedimentation rate determined for the 1985 core was assumed to be valid for the 1996 cores on the basis of similar profiles of bulk density and C content. As in the previous figure, cores taken before1996 are shown beginning at depths corresponding to the amount of sediment that would have accumulated in the years between 1996 and the time at which the core was taken. Error bars represent 95% confidence intervals. 1985 core, ●; 1996 cores, ○ and ■.



mentally added to the lake (Table 1). The difference between the amount of sulfur added to the lake (1175 kg S), the amount accumulated in the water column (575 kg; Fig. 2), and the excess amount (i.e., the amount beyond the flux that occurred before artificial acidification) lost to outseepage (175 kg) should equal the amount of sulfur stored in the sediments. These mass balance calculations suggest that 36% (425 kg) of the sulfur addition was stored in the lake sediments.

Only one sediment core was retrieved from the lake in 1990, the final year of acid additions, from which the above estimate of sulfur burial can be verified. Comparison of the 1990 core with a core retrieved from the same location in 1985 (Fig. 3*a*) shows that sediment sulfur concentrations increased up to 25%. The magnitude of the temporal changes in S concentrations (0.75–1.5 mg·g^{-1}) is larger than the combined uncertainty (95% confidence interval (CI) = 0.6 mg·g^{-1}) resulting from analytical precision (relative standard deviation (SD) = 4%) and sediment heterogeneity as assessed in replicate cores obtained adjacent to one another (Fig. 4). Even the large anthropogenic addition of sulfur to Little Rock Lake left a signal in the sediment that was only 2–2.5 times higher than background noise.

The mass of sulfur calculated to have been buried in the sediments between 1985 and 1990 is consistent with the mass that was lost from the water column. Integration of the sulfur mass in the 1990 core between sediment masses of 0 g·cm^{-2} and 0.65 g·cm^{-2} (i.e., 1935–1990 based on the sediment accumulation rate determined with ^{210}Pb in the 1985 core) and subtraction of the mass in the 1985 core in the corresponding depth interval indicates that 0.62 mg·cm^{-2} of S were stored in the sediments at this site between 1985 and 1990. The rate of S accumulation at the top of the 1985 core was 0.063 mg·cm^{-2}·year^{-1}; if this rate is multiplied by 5 years and subtracted from the additional sulfur found in the 1990 core, an "excess" accumulation of 0.31 mg S·cm^{-2} is calculated. If S storage in the sediments occurred evenly throughout the sediment deposition zone (about 60% of the north basin area, Baker et al. 1989), the core suggests that 180 kg of S was stored in the sediments between 1985 and 1990. Alternatively, if the ^{210}Pb focusing factor for this site (0.84; Baker et al. 1992) is used to extrapolate the accumulation rate in this core to the whole basin, a total burial of 360 kg S is calculated. These estimates (180–360 kg S) based on the sulfur concentrations in the 1990 core are less than the value calculated from the lake mass balance (425 kg) and suggest that 15–30% of the acid additions were neutralized by burial of sulfur in the sediments.

It cannot be stated unequivocally if the enhanced burial of sulfur resulted from sulfate assimilation by algae and subsequent burial of the organic matter or from fixation in sediments of microbially reduced sulfur. Only total sulfur rather than individual sulfur species were measured in the 1990 core because of the probability of changes in speciation during storage. Measurements of sulfur concentrations in seston for the period 1985–1988 showed no increase in sulfur content even though concentrations in the water column increased from 25 μM to 60 μM (Baker et al. 1989). Thus, it seems likely that the burial in the sediments of experimentally added sulfur resulted from fixation of microbially reduced sulfur. In a preliminary mass balance for Little Rock Lake, Baker et al. (1989) estimated that fixation of microbially reduced sulfur accounted for, at most, 50% of the total sulfur accumulation in the sediments. Rates of fixation of microbially reduced sulfur would have to increase by at least 50% to provide the observed increase in total sulfur accumulation of 25% in the 1990 core. Thus, results from Little Rock Lake support models that assume that rates of sulfate reduction increase with increasing sulfate concentrations in lake water (Baker et al. 1986; Kelly et al. 1987).

Release of sulfur from sediments

Release of sulfur from sediments might occur episodically, seasonally, or potentially over longer time periods. The long-term storage and release of sulfur from sediments was studied by comparison of cores collected in successive years from the same locations in Little Rock Lake. Sediment cores were taken at a 5-m site in the north basin before (1985), during (1990), and after (1992, 1996) acidification and at 7- and 9-m sites in the north basin before (1985) and after (1996) acidification. The sediment accumulation rates at the

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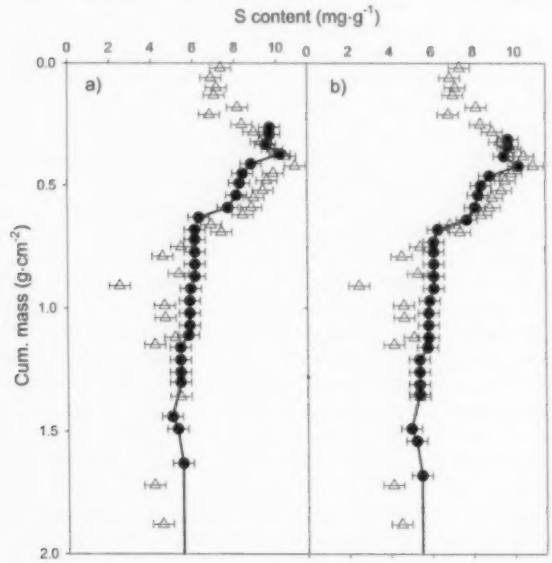
Table 2. Comparison of sulfur inventories in sediment cores from north basin of Little Rock Lake.

Water depth (m)	Year in which core taken	S inventory ($mg \cdot cm^{-2}$) above 1940 horizon[a] (A)	Expected S accumulation ($mg \cdot cm^{-2}$) between year of core sampling and 1996 (B)[b]	Sulfur inventory ($mg \cdot cm^{-2}$) expected in 1996 (C) ($C = A + B$)	C as a % of 1985-core inventory
5	1985	2.75	0.68	3.43	100.0
5	1990	3.53	0.42	3.95	115.3
5	1992	3.30	0.26	3.56	103.9
5	1996	3.61	0.00	3.61	105.3
7	1985	2.39	0.74	3.14	100.0
7	1996	3.33, 3.18	0.00	3.33, 3.18	100–106
9	1985	4.69	1.44	6.13	100
9	1996	6.21	0.00	6.21	101

[a]The sedimentation rate determined by ^{210}Pb dating in the 1985 core was assumed to remain constant for the period 1985–1996.
[b]The sulfur accumulation rate in the surface sediments (0–0.5 cm) of each core was assumed to remain constant for the extrapolation to 1996.

Fig. 5. Sulfur profiles in cores collected at 9-m water depth in the north basin of Little Rock Lake. The correspondence between the two cores collected 11 years apart and at locations ~100 m apart seems remarkable and suggests that no excess sulfur was stored in the sediments as a result of the experimental lake acidification. (*a*) The assumption is that the sedimentation rates for both cores were identical; (*b*) the sulfur peaks in both cores align, and such an adjustment would imply that the sedimentation rate at the 1996 site was 20% higher than the sedimentation rate in the 1985 core. 1985, ●; 1996, △. Error bars represent 95% confidence intervals.



1985 sites were determined with ^{210}Pb (CRS model) (Baker et al. 1992) and were assumed to have remained constant since that time. The historical sequence of cores at the 5-m site (Fig. 3) suggests that sulfur was initially buried in the sediments during lake acidification, but the sulfur has been released from the sediments after cessation of experimental acidification. The 1985 sulfur profile had a relatively constant total sulfur concentration (~5.5 $mg \cdot g^{-1}$) between depths of 0 and 0.5 $g \cdot cm^{-2}$ (corresponds to ~1940–1985). The 1990 profile had a subsurface peak with concentrations about 25% higher than those in 1985 (Fig. 3*a*). The 1992 profile had concentrations lower than in 1990 (Fig. 3*b*), and concentrations were further reduced in the 1996 profile (Fig. 3*c*). These results are consistent with an initial burial followed by release of S from the sediments.

Because the sediments become anoxic and sulfate reduction occurs within the upper centimetre of sediment at the 5-m site (Urban et al. 1994), the sulfur concentrations in the surface sediments should reflect the historical pattern of rates of sulfate reduction. If the sulfur concentrations in the surface sediments of the cores from the 5-m site are compared, they follow the same temporal trend exhibited by sulfate concentrations in the water column. The S concentration in the topmost increment of sediment (0.5 cm) increased from 5.4 $mg \cdot g^{-1}$ in 1985 to 6.1 $mg \cdot g^{-1}$ in 1990, and it decreased back to 5.8 $mg \cdot g^{-1}$ in 1992 and to 5.5 $mg \cdot g^{-1}$ in 1996.

Similarly, if the inventories (mass) of sulfur in the cores are compared, it appears as if an initial increase in sediment sulfur was followed by a net loss of sulfur. If a common lower horizon corresponding to 1940 is chosen and the amounts of sulfur that would have fallen between 1996 and the dates on which the cores were obtained (assuming the S sedimentation rate remained constant at the rate measured in surface sediments) are added to the inventories of S in each core (above the 1940 horizon), the inventory in the 1990 core is seen to be 14% greater than that in the 1985 core, and the inventories in the 1992 and 1996 cores return to within 5% of the inventory in the 1985 core (Table 2). At 7- and 9-m sites, no cores were taken in 1990 or 1992, but as for the 5-m site, the inventories of sediment sulfur in cores taken in 1985 and 1996 are within 6% of each other when compared in the fashion described above (Table 2).

The historical sequence of changes in the sediment cores (Fig. 3) suggests that sulfur is both gained and lost from a few centimetres below the sediment surface. Holdren et al. (1984) demonstrated through modeling that it is reasonable for the diffusive influx of SO_4^{2-} to be buried below the sediment surface. Baker et al. (1989) attributed the subsurface peak in sulfur concentrations at the 9-m site in Little Rock Lake to diffusion of sulfate to this depth. The 1996 core from the same 9-m site shows that this subsurface peak is being buried (i.e., the peak occurs at a greater depth in 1996 than in 1985; Fig. 5), which would imply that S fixation rates in the sediments must be lower now than they were in the past. Such a decrease in S incorporation into sediments

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Fig. 6. Seasonal cycle of SO_4^{2-}/Cl^- ratios (mole SO_4^{2-} : mole Cl^-) in the water column of the north basin of Little Rock Lake in 1996–1997. Ratios are highest in winter and lowest in summer as a result of sulfur uptake by biota in the water column and sediments.

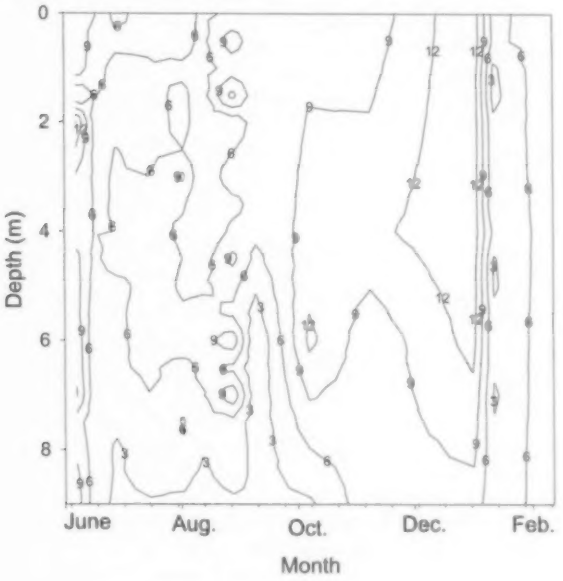
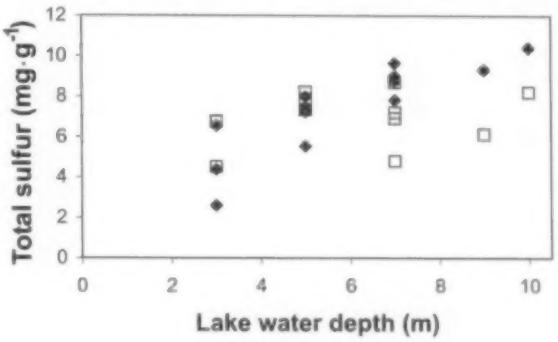


Fig. 7. Comparison of S concentrations in surface sediments (0–4 cm) of the north basin before (◆) and after (□) fall overturn. Sediments at water depths >5 m show a release of S after overturn.



is consistent with the nearly twofold decrease in atmospheric deposition of sulfate that has occurred in northern Wisconsin between 1985 and 1998 (V.C. Bowersox, National Atmospheric Deposition Program, NADP, Illinois State Water Survey, 2204 Griffith Drive, Champaign, IL 61820, unpublished data). At the 5-m site, rates of S fixation have decreased to such an extent that the peak in sulfur concentrations observed at a depth of 0.33 $g \cdot cm^{-2}$ (5 cm) in the 1990 core is diminished in 1992 and absent in 1996 (Fig. 3). One interpretation of this historical sequence would be that rates of S release from the sediments exceeded rates of fixation during the period 1990–1996. It has not been shown previously that sulfur can be lost from several centimetres below the sediment surface.

If the loss of sulfur from the sediments at the 5-m site is real, it happened largely within a 2-year period, 1990–1992. In other words, almost the entire increase in sediment sulfur inventory caused by experimental acidification may have been lost from the sediments within the first 2 years after cessation of experimental sulfate additions. Even though the S was stored at depths of 3–7 cm (corresponding to sediment ages of 20–40 years), it evidently still was susceptible to some loss mechanism. Seasonal oxidation is one possible mechanism for loss of sulfur from lake sediments (Kling et al. 1991).

There is considerable indirect evidence for seasonal loss of sulfur from sediments of Little Rock Lake. Both basins in the lake exhibit a seasonal cycle in sulfate concentrations and SO_4^{2-}/Cl^- ratios in the water column (Fig. 6); highest ratios occur during winter and lowest ratios occur in summer. Seasonal changes in lake volume counteract to some extent the seasonal changes in SO_4^{2-} concentrations; if the Cl^- ion behaves conservatively in the lake as argued by Urban et al. (2001), then the ratio of SO_4^{-2} to Cl^- should eliminate the confounding effect of lake volume changes and reveal only the changes in sulfate inventory in the lake (Fig. 6). Urban et al. (2001) showed that the monthly average SO_4^{2-} concentrations are highest in both basins in February; in the north basin, the average February concentration is 15 $\mu mol \cdot L^{-1}$ higher than the average August concentration, and in the south basin, the average February concentration is 6 $\mu mol \cdot L^{-1}$ higher than the average August concentration. The variability in the magnitude of these seasonal oscillations in concentrations is large; in some years, no seasonal change is observed, and in other years, the oscillation can be nearly twice the average. Because lake stage is lowest in summer (Rose 1993), the seasonal concentration differences are not driven by evaporative concentration. Rather the seasonal concentration changes are thought to result from seasonal storage in and release from sediments of about 200 kg S in the north basin and about 40 kg S in the south basin (Monte 1998; Urban et al. 2001).

In August 1996 and January 1997, surface sediment samples were collected to determine if the change in inventory of sulfur in the sediments could account for the seasonal pattern of sulfate concentrations observed in the water column. Sediments from the south basin showed no significant change in S concentrations in January compared with August. Similarly, in the north basin, all epilimnetic sediments (i.e., water depths ≤5 m) showed no seasonal change in S content (Fig. 7). However, all hypolimnetic sediments showed a clear decrease in S content after fall overturn (Fig. 7). In Little Rock Lake, it appears as if only those sediments underlying anoxic waters in summer will experience a release of sulfur after fall overturn.

The mass of sulfur estimated to have been released from the sediments of the north basin between August 1996 and January 1997 was 71 ± 47 kg, where the uncertainty (±47 kg) is a propagated error (95% CI) accounting for the variability in sediment S content and bulk density. Loss of organic rather than inorganic S was the major contributor to the change in sediment sulfur content in this year; however, in years with larger S release, inorganic S may make a larger contribution as was observed by Kling et al. (1991). The

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mass of sulfur released from north basin sediments in 1996 (71 kg) was smaller than the average seasonal change in S inventory in the water column of the north basin (~200 kg). However, no increase in sulfate concentration in the water column of either basin was measured in the winter of 1997. Thus it appears that the seasonal oscillation in S content of the water column was smaller than normal in 1996–1997; it seems likely that the release from the sediments also was smaller than normal.

In summary, experimental addition of sulfuric acid to the north basin of Little Rock Lake lowered the pH from 6.1 to 4.7. Six years after cessation of acid additions, the pH of the north basin had climbed back to 6.0, although the mass of sulfur in the water column of the north basin was still nearly 20% greater than the mass of sulfur before acid additions. Approximately 50% of the sulfate added to the lake disappeared from the water column through the combined processes of outseepage to groundwater, seston deposition and burial, and microbial sulfate reduction. A mass balance for S in the north basin suggests that 15% of the experimentally added S was lost to outflow and 36% (425 kg S) was lost to microbial sulfate reduction; burial of seston S was not observed to increase during the acidification.

Sediment cores indicated that the sediments were only a temporary sink for the sulfur. Cores collected at one location in the lake revealed that although a core collected in 1990 had sulfur concentrations 25% higher than did a core collected in 1985, cores collected in 1992 and 1996 had progressively less sulfur than the core from 1990. Sulfur concentrations in three cores collected in 1996 were equal to concentrations observed in cores from the same locations collected before acid additions. Considerable recycling of reduced sulfur from the lake sediments to the lake must occur.

Sulfate profiles in the water column suggested that some of this recycling occurs on a seasonal basis. The north basin experiences a depletion of sulfate in the deeper waters during summer, but concentrations peak during the winter. These seasonal fluctuations amount to nearly 15% of the total sulfur inventory in the water column of the north basin. Sediment cores revealed that sulfur is stored in surface sediments during summer and released after fall overturn. A total of 71 kg of sulfur was released from the sediments of the north basin during the winter of 1996–1997. It is not yet clear if this seasonal release merely represents mineralization of seston (85% of seston deposition is mineralized) or if it also contributes to the release of microbially reduced sulfur from the sediments.

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Tagging of Pacific herring *Clupea pallasi* from 1936–1992: a review with comments on homing, geographic fidelity, and straying

D.E. Hay, P.B. McCarter, and K.S. Daniel

Abstract: Nearly 1.6 million tagged herring (*Clupea pallasi*) were released in two separate programs (1936–1967 and 1979–1992) in British Columbia. Several thousand tags were released in each of 955 release sessions. Over 85% of the release sessions had subsequent recoveries. Almost 43 000 tags were recovered over all years. We re-assembled the tagging data into an electronic database, geo-referenced all tag release and recovery data, analysed spatial movements, and estimated straying and fidelity rates. The analyses do not wholly support the conclusions of previous work indicating high homing rates to local coastal areas. Estimates of fidelity, defined as the proportion of tags recovered in the same area as released, varied with the size of the geographic area used in the analyses. Fidelity rates are high for large areas, such as the Strait of Georgia (~10 000 km^2), but lower for small geographical areas, such as inlets or bays (~100 km^2). High fidelity is not necessarily evidence for "homing." Homing and fidelity are different biological processes and tagging cannot necessarily distinguish between them. Although fidelity rates for small areas are generally low, there are exceptions that may be evidence for the existence of biologically distinct populations in certain areas.

Résumé : Près de 1,6 million de harengs (*Clupea pallasi*) ont été marqués et relâchés dans le cadre de deux programmes de marquage de 1936 à 1967 et de 1979 à 1992 en Colombie-Britannique. Dans chacune des 955 opérations, des milliers de poissons marqués ont été remis à la mer. Plus de 85% de ces opérations ont donné lieu à des recaptures subséquentes. Au cours de ces années, près de 43 000 poissons marqués ont été repris. Nous avons réuni toutes ces informations dans une base de données électronique et nous avons relié toutes les données de marquage et de recapture à des coordonnées géographiques, ce qui a permis d'analyser les déplacements et d'estimer les taux d'errance et de fidélité. Les résultats de ces analyses n'appuient pas les conclusions de travaux antérieurs qui indiquent un fort taux de homing vers les régions côtières locales. Les estimations de fidélité, définies comme la proportion des poissons marqués recapturés dans la région où ils ont été relâchés, varient avec la surface géographique analysée. La fidélité est élevée pour les grands espaces géographiques, tels que le détroit de Georgie (~10 000 km^2), mais plus faible pour les espaces plus restreints, tels que les anses et les baies (~100 km^2). Une haute fidélité n'indique pas nécessairement un comportement de homing; la fidélité et le homing sont des processus biologiques différents et le marquage ne permet pas nécessairement de les distinguer. Bien que les taux de fidélité soient généralement faibles pour les régions restreintes, il y a néanmoins des exceptions qui peuvent laisser croire à l'existence de populations biologiquement distinctes à certains endroits.

[Traduit par la Rédaction]

Introduction

The issue of homing is a key part of an ongoing debate and dialogue about herring (*Clupea*) stock structure (e.g., Iles and Sinclair 1982; Stephenson and Kornfield 1990; Hay and McCarter 1997). A view held by most participants in this debate is that herring stock structure is related in some way to the geographical location of spawning areas. It is not clear, however, if some herring "home" in the same way that many salmonids species home by returning to natal spawning areas (Hasler 1966). "Natal homing"— the return to natal spawning areas—is a commonly understood use of the term "homing" and requires the fish to have the ability to memorize a natal area through imprinting or some other form of geographic memory developed during the early life stage.

The term homing also is used more broadly and, as discussed by McQuinn (1997), can be taken to mean a return of a spawning fish to the same spawning area used in previous years but not necessarily the one in which the fish lived as an egg or larvae or juvenile. This usage, perhaps better called "sexual" homing to distinguish it from "natal" homing, would apply to the way it was used by Wheeler and Winters (1984), who commented on homing in Atlantic herring (*Clupea harengus*). This type of homing requires that a herring develop a memory of its first spawning area or in some way develop associations with other individuals that will exhibit sexual homing. This usage also is seen in essays describing theories of herring population such as the member–vagrant hypothesis (Sinclair 1988) and the adopted-migrant hypothesis (McQuinn 1997). Repetitive interannual

Received April 28, 2000. Accepted March 16, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 4, 2001.
J15741

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 DOI: 10.1139/cjfas-58-7-1356 © 2001 NRC Canada

use of the same summer feeding areas or overwintering areas by herring that spawn in many different locations may also represent a form of homing, but not to spawning areas, and is not considered in the present paper. Implicit in these definitions, however, is the assumption that herring move or migrate because to home a fish must first move away; therefore, any usage of the term homing must involve some form of movement or migration. We suggest that this assumption often may not be warranted and may lead to incorrect conclusions about the prevalence and specificity of homing in herring.

This paper reports results on tagging experiments conducted from 1936 to 1992 in British Columbia (B.C.). We describe interannual changes in herring distribution to measure and describe "reproductive" homing behaviour. We show that estimates of homing are affected by assumptions about the geographic area (km^2) of release and recapture sites: estimates of homing are high, or inflated, if the geographical areas are large, and vice versa. We distinguish between homing and "geographic fidelity" and point out that recapture of nonmigratory herring in the same location as their release, which they may never leave, is not evidence of homing but could be misinterpreted as homing. Rather, recapture of tagged nonmigratory herring is evidence of geographic retention or fidelity.

Although herring tagging experiments have been conducted in B.C. for over six decades, it is only the most recent experiments (1979–1992), with external Floy® tags, that have specific dates of recapture. From 1936 to 1967, herring were tagged with internal "belly" tags. Although there were many recoveries, few had specific information on the date of recovery (Hourston 1982). Therefore, only anchor-tagging recoveries can be used to comment on the specific issue of homing to specific spawning sites during the spawning season, although much of the older tagging data provide reliable estimates of fidelity. We use anchor-tagging data to comment on the specific issues of (*i*) geographic fidelity and (*ii*) homing to previously used spawning sites.

Herring tagging data are organized according to geographical divisions of the B.C. coast based on spawning areas. We begin with a brief description of the major spawning locations and a description of the geographical divisions.

Materials and methods

Distribution of spawning sites in B.C. herring

The intertidal and shallow subtidal spawning areas of Pacific herring (*Clupea pallasi*) have been documented on the B.C. coast since the 1930s. Data on spawning sites are maintained in an electronic database that is updated annually at the Pacific Biological Station. Each year the cumulative length of spawning events is about 400–600 km (Hay and Kronlund 1987). Since the 1930s, herring have spawned on about 20% of the total B.C. coastline, but most spawning activity is clustered into a few key areas in each of the six main geographical regions of the B.C. coast (Fig. 1). Hay and Kronlund (1987) described a simple quantitative index of spawning that can be used to compare the relative spawn deposition among different areas of the B.C. coast (Fig. 1).

Description of herring tagging projects in B.C.

The earliest tagging programs (1936–1967) used metallic belly tags that were inserted into the body cavity and recovered with magnetic detectors in reduction plants. Release of belly tags stopped in 1967 with the closure of the reduction fishery. The development of the roe fishery in the early 1970s led to a renewal of a new herring tagging program in 1979 that used external anchor tags. Pilot studies examined recovery rates from fish plants and the tag retention and survival of tagged fish in captivity (Hay 1981). A description of all previous herring tagging programs in B.C. is presented in Daniel et al. (1999).

The tags

Most belly tags used from 1936 to 1967 were nickel-plated iron rectangles with rounded ends (approximately 19 mm long, 4 mm wide, and 1.6 mm thick) that were inserted into the body cavity through a small incision (Hart and Tester 1937). The Floy® anchor tags used from 1979 to 1992 were made of a plastic tube attached to a monofilament T-shaped end that was inserted into the dorsal musculature (Daniel et al. 1999). Both the belly tags and anchor tags had individual coding numbers so that recoveries could be traced back to the date and location of release.

Tagging data records

Almost 1.6 million tags were released from 1936 to 1991 (Appendix 1). Most tag recovery data from 1936 to 1957 were published annually in Provincial (B.C.) Government reports that are listed in detail in Daniel et al. (1999), which also lists sources of more recent results data, mainly manuscript reports from Fisheries and Oceans Canada Pacific Stock Assessment Review Committee (PSARC) working papers. There are different levels of precision about tag recovery information, particularly with respect to exact date and location of the recovery. The exact location and date of release is known for all tag releases but the accuracy and precision of tag recovery data varies. For nearly all belly-tagging data, we know only the "season" or year of recovery, although from review of historical catch data, it is clear that most fisheries, hence tag recaptures, were made between November and March. In the reduction fishery, the metal tags accumulated in the reduction chambers in processing plants and were not necessarily recovered for individual catches; therefore, such recovered belly tags may have come from several different statistical areas or many different sections, although for most the region was known. In contrast, exact recovery dates were recorded for most anchor tags.

Estimating the number of years-at-large

Although all tag release dates were recorded to the nearest day, recovery dates were recorded to the nearest day only for anchor tags (1979–1992). Recovery dates for most belly tags, released from 1936 to 1967, were recorded only to the nearest year. To estimate the approximate number of years-at-large for belly tags, we assumed that all belly tags with unknown recovery dates (day or month) but with a known recovery year were recovered at midyear (July 1) of the same year they were recovered. Therefore for belly tags released in July of the previous year, the estimate of years-at-large would be about 1 year. For tags released in October, the estimated time-at-large would be only 8 months or 0.66 years-at-large. For tags released in March, the estimated time-at-large would be 16 months or 1.33 years. Over 75% of all belly tags were released between mid-January to April (Appendix 2), so the estimated time-at-large for these tags, captured in the next calendar year after release, would range from about 1.25 (late April releases) to about 1.49 years (for very early January releases), and for our analyses, all would be rounded to represent 1 year at large. The time-at-large for tags recovered in two or more years was estimated in the same way. When rounded, all tags released between January and April and recovered in the same calendar year would be estimated to have been at large for a period of less than 1 year and be classified as zero (0) years-at-large.

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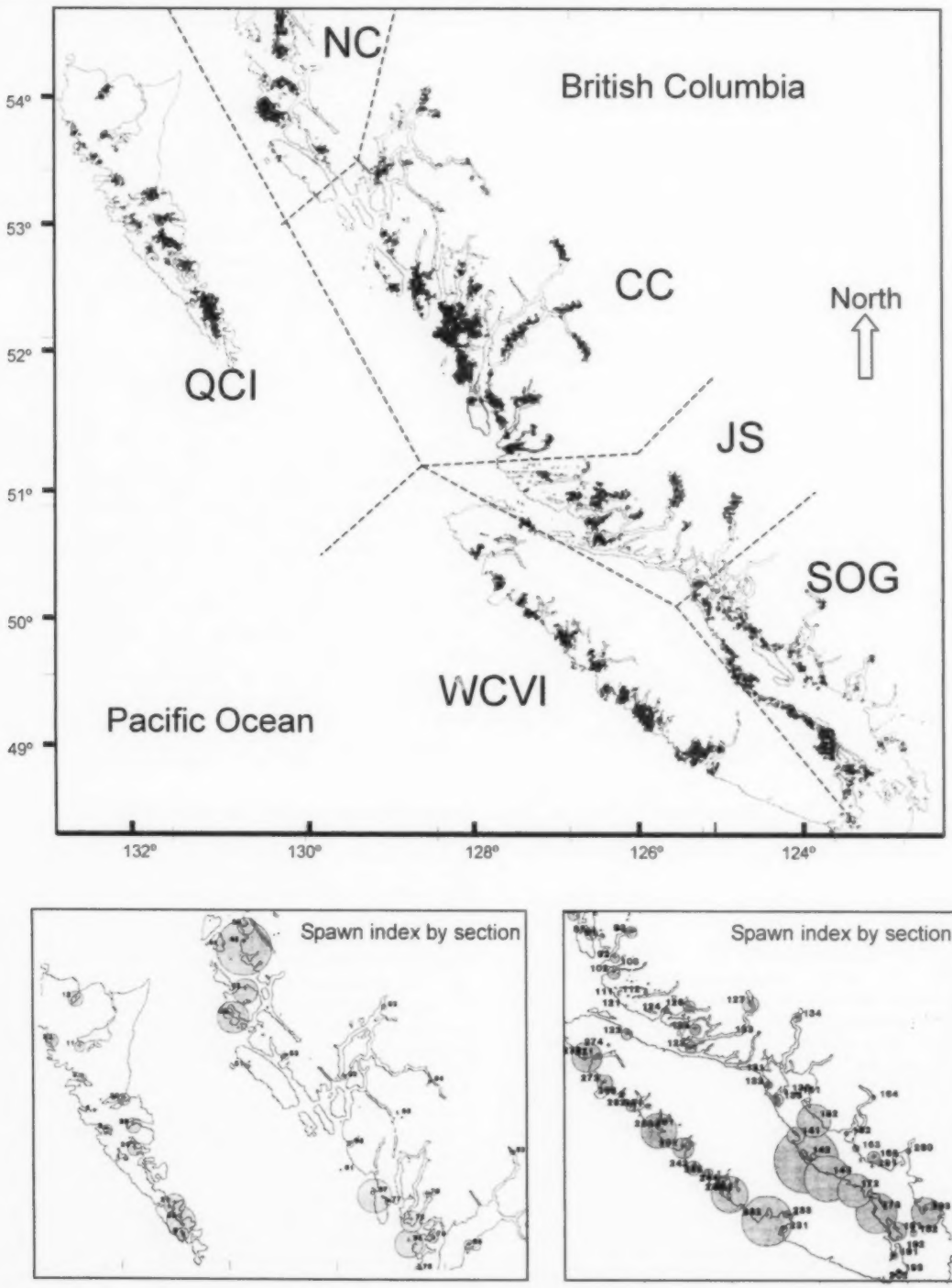
Fig. 1. The British Columbia coast showing all herring spawning areas (dark areas) and the six major regions identified as QCI (Queen Charlotte Islands), NC (North Coast), CC (Central Coast), JS (Johnstone Straits), SOG (Strait of Georgia), and WCVI (West Coast of Vancouver Island). The dark areas indicate all recorded spawning locations from 1936–2000 but do not differentiate the relative size or importance of spawning areas. This is indicated in the panels below by the shaded circles that show a relative index of spawn (Hay and Kronlund 1987) representing the approximate locations of major spawning areas.



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Estimating the geographic precision of recovery

The basic geographical unit for Fisheries and Oceans management of all species is a "statistical area," and about 30 are applicable to herring in coastal waters of B.C. (Fig. 2). Each statistical area is subdivided into "sections," designed specifically for herring management (Haist and Rosenfeld 1988). There are over 100 sections included in either tag release or recovery data (Table 1). In general, many of these sections comprise the smallest geographical unit that could define a "spawning ground," although in some instances, single spawning areas will overlap two or three different sections. In contrast, large sections, particularly some that include long fjords, may include two or more separate spawning areas. The smallest or most precise geographical unit used is a "location" or geographical name. There are about 536 locations used in the herring data release and recovery database (Table 1).

Statistical areas can be pooled into six larger areas called regions (Table 1), which correspond to large natural geographic groupings. The approximate sea surface area (km^2) for each section was estimated using Sigmascan© image analysis software. The areas of the larger geographical domains, statistical areas and regions, were then estimated as the sums of the areas of the component sections. Locations were only points on a chart, so sea surface areas for locations were not estimated.

Tag recovery information

During the reduction fishery tagging (1936–1967), processing plants sometimes were able to identify the tag origins according to the statistical area of the fishery, but the specificity of geographic recovery location varied. For many tags, the plants could determine only that recovered tags were from a potential group of statistical areas, such as between Statistical Areas 14 and 18. This range of statistical areas falls within the Strait of Georgia, one of six regions of the B.C. coast; therefore, in such instances, the Strait of Georgia (region) would be the most precise return information available. The six regions are Queen Charlotte Islands (QCI), North Coast Rupert District (NC), Central Coast (CC), Johnstone Strait (JS), Strait of Georgia (SOG), and West Coast of Vancouver Island (WCVI) (Fig. 2). For other tags, we could name the statistical area of recovery with certainty, but not the section or location. For many tags, no geographic recovery information was available. (Subsequent reference to statistical areas and sections are made by number corresponding to Fig. 2.)

Estimating rates of tag recovery

The location of each tag recovery was compared to the area of release at each of the four different geographic scales or domains: region, statistical area, section, and location. For each recovery, we estimated the number of years-at-large or the estimated mean number of years between release and recapture. Most belly tag recovery information was incomplete, with either the recovery date or exact location missing. Usually, however, there was at least partial information on the geographical region of recovery and the calendar year of recovery was known. Therefore, for any group of tag releases within 1 year, the rates of recovery in each of the following years can be estimated as the ratio N_y/N_{y-1}, where N is the number of recaptures after y and $y - 1$ years of release.

Estimating fidelity (F), straying (S), and immigration (I) rates

Estimates of fidelity are made for a specific time period (1 or more years) and are based on the geographic distribution of tag recoveries relative to the area of release. To estimate fidelity for a specific geographical domain d (i.e., a section, statistical area, section, or location), we let n_d represent the number of tags released and recovered within domain d, n_o equal the number released in domain d but recovered in all other domains (o), and t_d equal the total number of tags recovered from tag releases within domain d but recovered in all domains so that $t_d = n_d + n_o$. We let i_d represent the numbers of tags recovered in domain d but released in other domains. The ratio n_d/t_d is an estimate of area-specific fidelity (F) rate, which will be between zero and one, or between zero and 100 when shown as a percentage. F represents herring that were retained within domain d or that left and returned to domain d before recapture. The ratio n_o/t_d is an estimate of straying (S) from domain d (or emigration), and the ratio $i_d/(n_d + i_d)$ is an estimate of immigration (I), or the proportion of fish in domain d that are immigrants from other domains. Rates of F, S, and I can be estimated for different geographical scales or domains including locations, sections, statistical areas, or regions. Further, F, S, and I can be estimated for different combination of years of release, or estimated according to the years that tags were at large. We show rates of F, S, and I for herring that have been at large for 1 year or more and compare F among different geographic scales (domains). For analyses of homing, we examine a subset of the data that restricted tag release and recovery to March or April, corresponding to the spawning times, and to tags that had been at large for 1 year or more. All but a few of the data in this subset consisted of anchor tags, released and recovered in the roe fishery.

Results

Area of geographical divisions

Table 1 shows approximate area (km^2) for each region, statistical area, and section. The regions vary from about 3000 km^2 to 10 000 km^2. Most statistical areas are between 500 and 2500 km^2, and most sections are less than 300 km^2. There is overlap in sizes among the respective geographical divisions, with some statistical areas being larger than regions, and some sections larger than statistical areas. Also, these estimates of area (km^2) are approximate, particularly because the position of lines separating the many divisions from open water is arbitrary (Fig. 2). The sums of area for the sections are used to estimate the areas of statistical areas. The areas of the regions shown in Table 1 refer only to the areas in proximity to spawning areas (i.e., sections). The actual area (km^2) for all regions except the Strait of Georgia is larger than indicated here and includes areas of open water in Hecate Strait, or the open Pacific off the west coast of Vancouver Island.

Recovery numbers and spatial and temporal distribution of released and recovered tags

Between 1936 and 1991, tags were released in a total of 955 different capture and release sessions (Appendix 1). A total of 1 595 249 herring tags were released, including over one million belly tags released from 1936 to 1967 and over 500 000 anchor tags released between 1978 and 1991. Approximately 85% of the 955 tag release sessions resulted in some eventual tag returns and the overall mean recovery rate of the 1.6 million was 2.68%, but this varied annually from a low of about 0.5% to a maximum of over 11% (Appendix 1). For both belly and anchor tags, about 76% were released between February and April, during the spawning season (Appendix 2), and about 15% of the belly tags were released in the summer months. The year of recapture is known for nearly all belly tags returns but the month and day are unknown for most. Most anchor tags (>85%) were recovered in March and April (Appendix 2). A total of 42 767 tags were recaptured, including 37 326 belly tags and 5441 anchor

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Fig. 2. The British Columbia coast showing two levels of geographical divisions called regions and sections. Each of the six regions is shown in detail in separate panels: (*a*) Queen Charlotte Islands, (*b*) North Coast, (*c*) Central Coast, (*d*) Johnstone Straits, (*e*) West Coast of Vancouver Island, and (*f*) the Strait of Georgia. Three-digit-numbered subdivisions within each region indicate different herring sections. Intermediate-sized statistical areas (see Table 1) consist of one or more sections and can be identified as the first two digits in the numbers shown for each section. Not shown are the 500 different locations that were recorded as tag release or recovery sites.

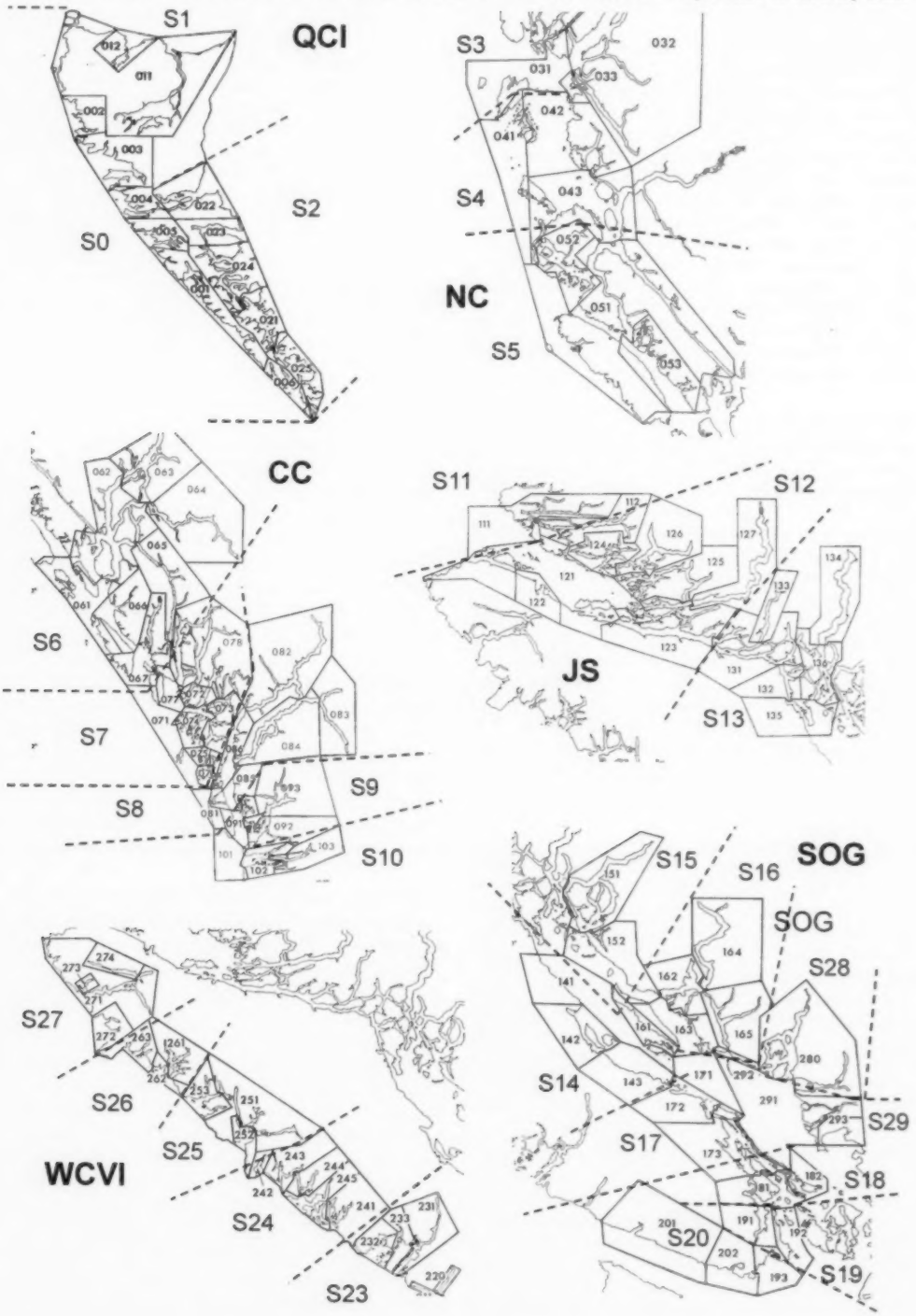

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Table 1. The relationship between regions, statistical areas, sections, and locations.

Region	Area (km²)	Statistical areas			Area of sections (km²)		Number of locations
		Code	Area (km²)	No. of sections	Minimum	Maximum	
QCI	4 361	S0	1 409	6	138	380	15
		S1	1 169	2	326	843	1
		S2	1 783	5	162	535	31
NC	5 230	S3	1 267	3	54	647	17
		S4	2 210	3	706	765	25
		S5	1 753	3	316	1 108	23
CC	11 123	S6	3 822	7	246	1 007	25
		S7	3 159	8	113	1 212	56
		S8	1 594	6	62	407	5
		S9	600	3	155	238	5
		S10	856	3	115	561	3
		S11	1 092	2	213	879	0
JS	5 105	S12	3 634	7	207	1 591	26
		S13	1 471	6	83	363	45
SOG	9 490	S14	1 597	3	272	953	33
		S15	1 029	2	465	564	13
		S16	1 168	5	150	403	7
		S17	1 130	3	180	554	56
		S18	581	2	289	292	20
		S19	762	3	73	350	9
		S20	968	2	310	658	4
		S21	70	1	70	—	4
		S28	494	1	494	—	2
		S29	1 691	3	55	1 525	1
WCVI	3 192	S22	38	1	38	—	0
		S23	653	5	196	255	41
		S24	663	1	50	246	21
		S25	600	3	130	252	24
		S26	476	3	145	183	12
		S27	762	4	30	428	12

Note: The six major regions are QCI (Queen Charlotte Islands), NC (North Coast), CC (Central Coast), JS (Johnstone Straits), SOG (Strait of Georgia), and WCVI (West Coast of Vancouver Island). The areas of the regions and statistical areas (under column Code, corresponding to Fig. 2) and minimum and maximum sea surface areas of sections within each statistical area are expressed in km². The numbers of different sections and locations, applicable to release of recovery of tags, is shown in far right.

tags. Of these recaptures, however, about 9400 were made within the same year as the release.

Rates of recovery: recoveries versus releases

For each year, the annual recovery rate represents tags released in a single year but recovered from over a number of different years. Table 2 shows the numbers of returns by the year of release and the number of years between the release and recapture. Most belly tags were recovered after 1 year at large but many were recovered over several years and a few were at large for 10 years. We cannot rule out, however, the possibility of some delays between date of the actual recovery of a tag from a plant and the date that it was forwarded to the laboratory. For releases with a single year, recovery rates can be estimated from the number of recaptures (N) after y years of release (N_y), divided by the number of recaptures a year later (N_{y-1}) after $y - 1$ years of release. The estimate of N_y/N_{y-1} is consistent with an approximate rate of 0.32 for belly tags the first 3 years (Table 3). This estimate would be affected by several factors, including annual fishing rates, the numbers and locations of tags released, natural mortality, tag retention, and tag detection. The rate of anchor tags recovery after the first year was lower than belly tags. A total of 81 anchor-tagged fish were recaptured after 2 years, or about 17% of the number (482) captured in the previous year. The lower rates of capture in the anchor-tagged fish could reflect (*i*) lower fishing rates during the roe fishery of the 1980s and 1990s; (*ii*) higher mortality rates of tagged fish (some tags were returned from salmon anglers who found the tags in salmon guts); and (*iii*) shedding of tags (Hay 1981) and incomplete reporting (Haegele 1990).

Geographic fidelity

Table 4 shows the release and recovery of all tags, for all times at large (1 day to 10 years). Herring movements were extensive: tags released in each region were recovered in nearly all other regions, but most tags were recovered in the same region in which they were released. Table 4 also shows some release and recovery sites in U.S. waters, although the numbers are low and are not included in the subsequent analyses. Table 5 shows a subset of the data restricting tag recoveries to those at large for 1 or more years and (similar to the subset used by Hourston 1982) limits the period of tag releases to the months of January to April. Table 5 shows es-

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Table 2. Total number of tag recoveries shown by the numbers of years between release and recapture.

Year of Release	Years between release and recapture											
	0	1	2	3	4	5	6	7	8	9	10	Total
1936	43	3	5	2	0	0	0	0	0	0	0	53
1937	152	770	29	1	1	0	0	0	0	0	0	953
1938	0	352	108	7	2	0	0	0	0	0	0	469
1939	570	540	112	19	2	0	0	0	0	0	0	1 243
1940	65	664	161	39	20	2	1	0	0	0	0	952
1941	0	288	111	50	9	1	2	0	1	0	0	462
1942	0	112	130	16	23	0	2	1	0	0	0	284
1943	0	516	79	20	5	8	0	1	0	0	**0**	629
1944	0	352	75	45	23	11	4	1	1	**0**	2	514
1945	0	528	117	125	97	20	24	12	**0**	2	1	926
1946	0	564	295	102	16	5	7	**0**	0	1	0	990
1947	0	1 779	766	129	26	20	**0**	0	0	0	0	2 720
1948	0	2 184	287	82	68	**0**	6	2	1	0	0	2 630
1949	0	688	261	140	**0**	16	1	1	0	0	0	1 107
1950	0	1 919	1 096	**0**	113	20	8	5	0	0	0	3 161
1951	0	3 401	**2**	525	55	38	19	0	1	3	0	4 044
1952	1	**4**	1 216	123	165	59	2	4	0	0	0	1 574
1953	**1**	2 687	409	497	154	3	12	2	0	0	0	3 765
1954	0	1 696	1 109	211	4	31	2	4	0	0	0	3 057
1955	0	879	305	24	7	0	0	0	0	0	0	1 215
1956	218	945	91	25	5	0	0	0	0	0	0	1 284
1957	0	68	108	22	24	0	0	0	0	0	0	222
1958	0	30	6	0	0	0	0	0	0	0	0	36
1959	0	0	0	0	0	0	0	0	0	0	0	0
1964	242	2 310	911	307	0	0	0	0	0	0	0	3 770
1965	0	1 091	107	0	0	0	0	0	0	0	0	1 198
1966	21	0	8	0	0	0	0	0	0	0	0	29
1967	0	0	0	0	0	0	0	0	0	0	0	0
1979	29	4	0	0	0	0	0	0	0	0	0	33
1980	79	38	23	2	2	1	0	0	0	0	0	145
1981	622	135	14	8	3	0	0	0	0	0	0	782
1982	570	47	7	0	0	0	0	0	0	0	0	624
1983	234	9	0	0	0	0	0	0	0	0	0	243
1985	73	3	0	0	0	0	0	0	0	0	0	76
1986	300	0	0	0	0	0	0	0	0	0	0	300
1988	264	12	4	0	0	0	0	0	0	0	0	280
1989	505	71	26	0	0	0	0	0	0	0	0	602
1990	1 402	141	7	0	0	0	0	0	0	0	0	1 550
1991	780	22	0	0	0	0	0	0	0	0	0	802
All	6 171	24 852	7 985	2 521	824	235	90	33	4	6	3	42 724

Note: The second column "0" indicates that less than 1 year transpired between release and recapture. The column "Total" shows all recoveries for each release year. In 1953, an industry strike reduced catches to nearly zero. The effect of that low catch is seen as a low return of tags released in previous years (in bold). The period of anchor-tag release is 1979–1991. The total is slightly lower than in Table 1 and Appendix 2 because the return years for some tags are unknown.

timates of F, S, and I as percentages. Based on 25 147 recoveries, most regions have approximately similar estimates of F and I. The estimates of fidelity within regions are high, with an $F > 90\%$ in three regions. These estimates for regions are similar to those presented by Hourston (1982).

The relationship between fidelity and geographic size of the domain used for analysis (areas of release or recovery (in km^2)) is shown in Fig. 3. Regions have the highest mean fidelity, followed by statistical areas and sections. Fidelity for nearly all locations is low and F estimates can be examined according to the sea surface area of each geographical domain (Fig. 4). Regions, with the largest sea surface area, have the highest mean fidelities. Locations, with the smallest sea surface areas, have the lowest mean fidelities. There is some overlap, however between the smallest and largest domains in each category. Estimates of fidelity do not appear to be affected by the numbers of years at large (Fig. 5), although there may be a decline in fidelity with time in some statistical areas. Some statistical areas and sections have high (>50%) fidelity estimates, but in some of these instances, the estimate may be based on very few recoveries. Figure 6 shows the relationship between mean fidelity and

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Table 3. Summary of the number of tags recovered after 0–10 years at large.

Years free	All tags		Belly tags		Anchor tags	
	Number recovered	Frequency n_y/n_{y-1}	Number recovered	Frequency n_y/n_{y-1}	Number recovered	Frequency n_y/n_{y-1}
0	6 171	—	1 313	—	4 858	—
1	24 852	—	24 370	—	482	(0.099)
2	7 985	0.321	7 904	0.324	81	0.168
3	2 521	0.316	2 511	0.324	10	0.123
4	824	0.326	819	0.326	5	
5	235	0.286	234	0.286	1	
6	90	0.383	90	0.385		
7	33	0.367	33	0.367		
8	4		4			
9	6		6			
10	3		3			
Totals	42 724		37 297		5 437	

Note: Data are shown for both tag types combined and belly and anchor tags separately. The frequency is the number of tags recovered in 1 year as a proportion of the number of tags recovered in the previous year. Note that the totals are slightly smaller than in Appendix 1 because of uncertainties about the recovery year for some tags.

Table 4. The number of recaptures of all tags shown by region.

Release region	Recovery region								
	UNK	QCI	NC	CC	JS	SOG	WCVI	USA	All
QCI	747	**2 885**	146	104	0	9	12	0	3 903
NC	679	204	**3 098**	220	18	15	11	3	4 248
CC	1 767	118	551	**8 249**	52	37	80	1	10 855
JS	536	0	4	369	**801**	142	22	0	1 874
SOG	2 922	7	12	64	282	**3 494**	287	4	7 072
WCVI	1 644	26	16	175	18	458	**12 398**	10	14 745
OFFS	16	0	0	0	0	45	9	0	70
All	8 311	3 240	3 827	9 181	1 171	4 200	12 819	18	42 767

Note: Columns indicate regions of recovery and rows indicate regions of release. The recovery location of 8311 tags was unknown (shown under column "UNK"). Release region "OFFS" refers to offshore releases. Region USA refers to a few recoveries from Washington State or Alaska. Tags recovered in the same area as the release are shown in bold. Regions: Queen Charlotte Islands (QCI), North Coast Rupert District (NC), Central Coast (CC), Johnstone Strait (JS), Strait of Georgia (SOG), West Coast of Vancouver Island (WCVI).

the number of tag returns for statistical areas (Fig. 6*a*) and sections (Fig. 6*b*). The total numbers of tag returns (defined as n_t in Methods and materials) to some areas smaller than regions (statistical areas, sections, and locations) are low and fidelity estimates could be misleading in these instances.

Herring movements, area-specific fidelity, and homing to spawning areas

Fidelity rate varies with geographical scale. After 1 or more years at large, between 4 and 39% of herring released between January and April strayed to different regions (Table 5). Straying rates were higher for smaller domains with about 40% among statistical areas, 83% among sections, and almost 99% among locations (Fig. 3). These estimates are means, however, and a few sections had relatively high fidelity rates, which indicates that some individuals were recovered in nearly the exact place of tagging and release, even after a period of years.

High fidelity does not necessarily indicate high homing. From surveys made in the summer, we know that some herring are widely distributed in nearshore shallow waters as well as on the continental shelf. Perhaps some herring do not migrate far, if at all, from their natal spawning areas. If so, we cannot use tag returns to distinguish between fidelity rates associated with homing and those that reflect a sedentary (nonmigratory) life history, and we suggest that such a distinction is not possible in some other areas, unless there were unequivocal evidence that all herring were migratory.

The most restrictive data of our analyses of the tag returns were obtained by selecting only tag recoveries that were at large for 1 or more years and released and recovered during a 2-month period corresponding to the spawning season (March and April). Only 285 tag recoveries fit these criteria, and all are from the anchor-tagging records, where information on exact dates and location of some tag recoveries was available (Table 6). Because most of these herring were captured on the spawning grounds or in the immediate vicinity, F could be interpreted as the best estimates of homing available from any of the tagging data from B.C. For most statistical areas, there is independent evidence that herring migrate to and away from spawning areas, probably to and from offshore feeding areas or overwintering areas (Table 6).

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Table 5. The number and percentage of releases and recoveries for each region for herring released between January and April and at large for 1 year or longer.

	Recovery						
Release area	QCI	NC	CC	JS	SOG	WCVI	All releases
QCI	**1 582**	49	61	0	2	4	1 698
%	**93.17** (*F*)	2.89	3.59	0.00	0.12	0.24	100.00
S	**6.83**						
I	**11.96**						
NC	121	**1 864**	172	14	12	5	2 188
%	5.53	**89.19** (*F*)	7.86	0.64	0.55	0.23	100.00
S		**10.81**					
I		**20.78**					
CC	86	425	7 188	34	25	49	7 807
%	1.10	5.44	**92.07** (*F*)	0.44	0.32	0.63	100.00
S			**7.93**				
I			**9.33**				
JS	0	1	367	**711**	60	15	1 154
%	0.00	0.09	31.80	**61.61** (*F*)	5.20	1.30	100.00
S				**38.39**			
I				**32.16**			
SOG	0	5	45	272	**1 807**	192	2 321
%	0.00	0.22	1.94	11.72	**77.85** (*F*)	8.27	100.00
S					**22.15**		
I					**16.11**		
WCVI	8	9	95	17	248	**9 602**	9 979
%	0.08	0.09	0.95	0.17	2.49	**96.22** (*F*)	100.00
S						**3.78**	
I						**2.69**	
All recoveries	1 797	2 353	7 928	1 048	2 154	9 867	25 147

Note: The two rows show the numbers and percentage of tags recovered in each region. Tags recovered in the same area as the release are shown in bold. The estimates of *F* (fidelity), *S* (straying), and (*I*) immigration are shown for each region. Regions: Queen Charlotte Islands (QCI), North Coast Rupert District (NC), Central Coast (CC), Johnstone Strait (JS), Strait of Georgia (SOG), West Coast of Vancouver Island (WCVI).

Fig. 3. Comparison of fidelity rates. The symbols show the mean fidelity for regions (solid circles), statistical areas (open circles), sections (solid squares), and locations (open squares). The overall mean for each geographic category is shown by the largest symbols, which connect the different geographical categories. Within each group, the array of points is jittered horizontally to reduce overlap but there is considerable overlap of symbols among sections and locations with low fidelity (lower right corner).

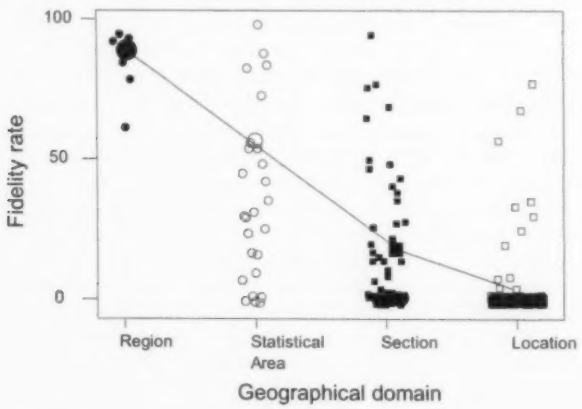
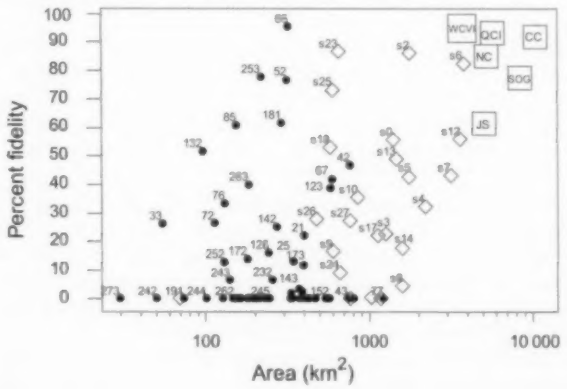


Fig. 4. Tag fidelity rates arrayed by the sea surface area (km^2) for regions (open rectangles), statistical areas (open diamonds), and sections (solid circles). The numbers beside each symbol represent the region, statistical area, or section as shown in Fig. 2.



For instance, in SOG, many years of summer surveys have failed to find many adult herring present, although juvenile herring abundance in SOG is high (Haegele 1997). Table 6 shows that five statistical areas (2, 5, 7, 14, and 23) all have high (>70%) homing estimates, although the sample size for Area 14 is low. A concern with these estimates, however, is that the same statistical areas that have high fidelity rates also are the main areas where closely regulated commercial

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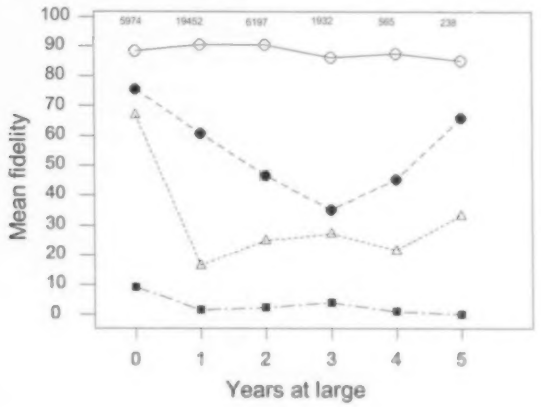
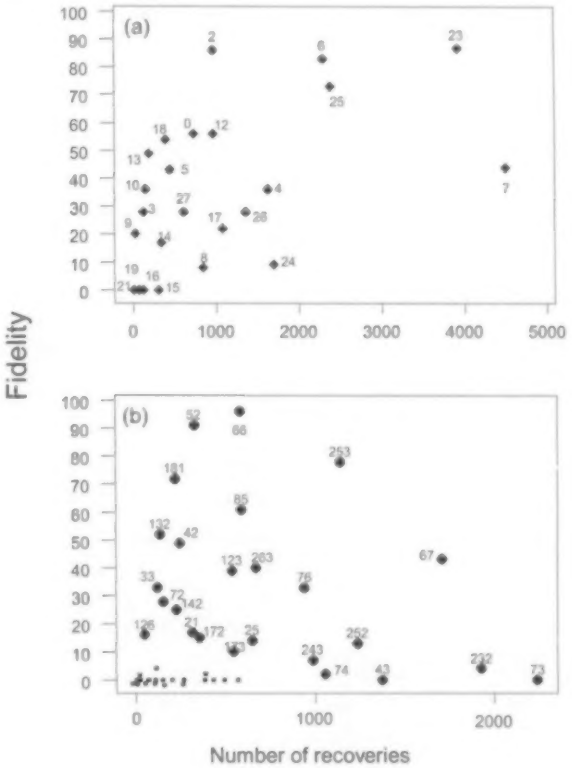
Fig. 5. Mean fidelity for regions (open circles), statistical area (solid circles), sections (open triangles), and locations (solid squares) shown according to the number of years at large. The numbers at the top of the panel show the number of tag recoveries used for each estimate.



roe fisheries occur, and no fisheries occur in most of the statistical areas with low fidelity estimates; therefore, these fidelity rates estimates may be inflated. There is indirect evidence of this in the form of relatively high immigration rates for many statistical areas, many exceeding 50% (shown at the bottom of Table 6). Therefore, we see a pattern of high fidelity and immigration rates in statistical areas with fisheries, and lower rates (but few tag recoveries) in areas with little fishing activity (Table 6). We suspect that this pattern may be explained by the fact that anchor tags were released over a broad geographic area that included many statistical areas but tag recoveries were confined to relatively limited number of areas where roe fisheries were conducted. The probable effect of this is an overestimate of fidelity for statistical areas with fisheries and an underestimate for those without, or with only small fisheries. The probable bias in Table 6 that applies to statistical areas probably is less of a concern when estimating for regions. Throughout nearly all years of anchor tagging, roe fisheries occurred in each region and with a similar catch rate in all, estimated at about 20% (Schweigert 1993).

In spite of these limitations, the results make a convincing case that some herring do indeed home to previously occupied spawning grounds and that the homing is made with the geographical precision of the approximate size (sea surface area) of statistical areas (Table 1). Table 6 shows that many herring do not home with such precision and presumably change spawning areas between years: over 20% moved to different spawning areas between regions. Some may argue, however, that there are other explanations for the apparent interannual changes in spawning areas. One alternate explanation is that some herring may make fast migrations immediately before spawning, so that the 2-month period (March–April) used to select the data from Table 6 is too broad and it is unreasonable to assume that all herring will be confined to spawning areas during this time. To this we would reply that based on past observation of roe fisheries, spent Pacific herring appear to leave spawning areas quite rapidly after spawning. Although we are uncertain about the migration

Fig. 6. Mean fidelity for statistical areas and sections by number of recaptures. These estimates represent tags released during March and April and recovered 1 or more years later. The broken lines indicate fidelity estimates above and below 50%. (*a*) Statistical areas. The numbers beside each symbol (solid diamonds) indicate the statistical area as shown in Fig. 2. Several overlapping symbols in the lower left corner indicate areas with low fidelity and recoveries. (*b*) Sections. The numbers beside each symbol (solid circles) indicate the individual section as shown in Fig. 2. Sections with low fidelity and recoveries are shown in the lower left corner where the size of the symbol is small to reduce overlap.



routes or immediate destinations, we do not believe that spent herring travel to other spawning areas, and roe fisheries occur only in the immediate vicinity of spawning areas. Therefore, we think it is reasonable to conclude that Table 6 shows evidence that some Pacific herring change spawning areas among years. Such a conclusion also is consistent with other observations of spawning and we have noted frequent occurrences of spawning on "new" grounds in some years, as well as abandonment of long-used spawning grounds (Hay et al. 1989).

Discussion

Homing and fidelity: implications of geographic scales on analysis

Fidelity rates depend on geographic scale used in the analysis: large areas have high fidelity rates and vice versa. Fidelity in exceptionally large areas, such as the entire B.C.

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Table 6. Estimates of homing to statistical areas of release and recovery during the spawning period, March–April, after 1 year or more at large.

Releases (region and statistical area)		Recoveries (region and statistical area)																
		QCI		NC			CC		SOG				WCVI			All	% *F* (statistical area)	% *F* (region)
		0	2	3	4	5	6	7	14	15	17	28	23	24	25			
QCI	0	**10**	13	1	—	—	—	3	1	—	—	—	1	—	—	29	**34.4**	**77.3**
	2	2	**33**	3	—	3	—	3	1	—	—	—	1	—	—	46	**71.1**	
NC	3	—	—	**5**	3	6	—	2	—	—	—	—	1	—	—	17	**29.4**	**91.7**
	4	—	—	3	**3**	2	—	—	—	—	—	—	—	—	—	8	**37.5***	
	5	—	—	—	1	**10**	—	—	—	—	—	—	—	—	—	11	**90.9**	
CC	6	1	1	—	—	—	—	8	—	—	—	—	1	—	—	11	**0**	**80.7**
	7	4	4	—	—	1	1	**76**	1	—	1	—	5	—	1	94	**80.8**	
	8	1	1	—	—	—	—	7	—	—	—	—	—	—	—	9	**0***	
	9	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	**0***	
JS	13	—	—	—	—	—	—	—	1	1	—	—	—	—	—	2	**0***	**0***
SOG	14	—	—	—	—	—	—	—	**5**	—	1	1	—	—	—	7	**71.4***	**83.3**
	15	—	—	—	—	—	—	—	1	—	1	—	1	—	—	3	**0***	
	16	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	**0***	
	17	—	—	—	—	—	—	1	4	—	—	—	1	—	—	6	**0***	
	18	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	**0***	
WC	23	—	1	—	—	—	—	—	—	—	—	—	**13**	—	2	16	**81.2**	**87.2**
	24	1	1	—	—	—	—	1	—	—	—	—	11	**1**	3	18	**5.5**	
	25	—	—	—	—	—	—	—	—	1	—	—	3	—	—	4	**0***	
	27	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	**0***	
All		19	54	12	7	22	1	102	16	2	3	1	39	1	6	285	**57.5**	**81.7**
% *I* (statistical area)		47.3	**38.8**	**58.3**	**57.1**	**54.5**	—	**25.4**	**68.7**	—	—	—	**66.6**	—	—			
% *I* (region)		**20.5**		**19.5**			**8.8**		**31.8**				**26.1**					

Note: Underlined numbers show regions and bold numbers show numbers recovered in the statistical area as release. In this table, the estimate of fidelity also is an estimate of homing. Fidelity (*F*) is shown on the far right for statistical areas and regions. Immigration rates (*I*) to recovery areas and regions are shown at the bottom for statistical areas (where $F > 0$) and regions. Asterisks indicate small (<10) numbers. The overall homing rate is 81.7% for regions and 57.5% for statistical areas. Regions: Queen Charlotte Islands (QCI), North Coast Rupert District (NC), Central Coast (CC), Johnstone Strait (JS), Strait of Georgia (SOG), West Coast of Vancouver Island (WC/WCVI).

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coast or the Gulf of Alaska, as areas of release and recovery, would always approach one (1). At other extremes, fidelity of small geographic units (e.g., locations or smaller) will approach zero (0). The question of biological interest is the spatial scale at which fidelity begins to increase above 0 and when it approaches 1. From this study, it is clear that regions, with an approximate area of 5000 – 10 000 km^2, have an F of about 80–90%. At the other extremes, there are almost no sections, except Section 33 with a low number of returns, with areas <100 km^2 that have detectable fidelity above 0. There are, however, a number of sections with fidelity estimates between 10% and 80% that are approximately 200–500 km^2 in sea surface area. At about 1000 km^2, there are a number of sections and statistical areas that have F estimates in the range of 20% to 60%. Wheeler and Winters (1984) showed estimates of homing rates from 65% to 93% (mean = 81%) based on returns to coastal areas ranging in length from 100 km to 500 km (mean = 276). There are several ways these estimates can be compared to B.C. fidelity estimates. The entire province has a total coastline of about 25 000 km, so the linear coastline of each of the six regions would then be about 4000 linear km and each statistical area would be about 800–1000 linear km. These linear lengths, however, do not provide a reasonable basis for comparison because we recognize that the total spawning areas are only a fraction of the total sea surface area. In general, herring have spawned on about 5000 km or 20–25% of the total B.C. coastline. Therefore, if we adjust the linear coastlines to reflect this, each region and statistical area would consist of about 400 and 100 linear km of spawning area, respectively. Viewed in this way, the geographical dimensions of Newfoundland coastline required to support fidelity rates of 80% are approximately similar to those of B.C. herring and would have about 80–100 linear km of spawning coastline.

Presently there are concerns that there may be distinct stock units within some of the major assessment areas (regions) used to manage the B.C. herring roe fishery. Our results do not address that issue but point to additional information requirements. For example, the tag recovery data indicate that about 10–20% of herring move between regions each year. These movements may be episodic (Hay et al. 1999) and more extensive in some years than in others. Future short-term tagging programs may not detect episodic movements, but such movements may have significant impacts on some aspects of population dynamics and differentiation. In particular, there appears to be a net direction of fish moving northwards in some years (Hay et al. 1999), particularly from CC to NC, with about 20% of the tagged herring recovered in NC released in other regions.

Implications for genetic analyses

Spawning biomass estimates in the last decade are high for most areas (Schweigert et al. 1998) but spawning has declined in some local areas (Hay and McCarter 1998). There are suggestions that declines in local spawning are caused by the reduction of local, nonmigratory, genetically distinct local populations from fishing or other causes. O'Connell et al. (1998), reporting on genetic structure of herring populations in Prince William Sound (PWS), Alaska, concluded that herring were genetically differentiated and reproductively isolated among three areas within PWS, which is approximately the same size as SOG at about 10 000 km^2. These putatively distinct Alaskan populations are not geographically isolated in remote inlets or fjords but are described as occupying different parts of PWS. O'Connell et al. (1998) acknowledge that there may be exchange of individuals among these populations but suggest that only a fraction of the strays that intermingle among the populations represent "genetically effective migrants." In support of their argument, O'Connell et al. (1998) cite Hourston's (1982) estimate of the B.C. herring homing rate of 83.6% as an estimate that may apply to PWS. Probably a better geographic comparison for PWS would have been an estimate of fidelity for statistical areas within regions because these correspond more closely in size and topography with the subdistricts within PWS described by O'Connell. Using statistical areas as the basis for comparison, it is probable that F would not exceed 60%. Also, our estimates of I for many statistical areas, estimated independently of F, may exceed 40%. If these estimates of F are roughly correct, it would be surprising if herring populations could maintain genetic differences when the annual exchange rate may reach 40% or higher.

Limitations and strengths of the present data and analysis

We acknowledge that the estimates of F in this paper, as well as Hourston's (1982) estimate of homing, may be biased and could be overestimated in areas with the greatest catches and lowest in areas with the smallest catches. For instance, if herring were only tagged and released in, for example, two different areas A and B, but if the fishery (hence recaptures) were limited to one area (A), then the estimate of fidelity in A would be 100%, even if the herring mixed completely among both areas. (In part, this type of bias is a concern for the numbers in Table 6.) The opposite also holds: if there were a high (>90%) fidelity to B, with the remainder (10%) straying to A, a low catch rate in B and a large catch rate in A would underestimate fidelity or homing to area B. To correct for this potential bias, analysis of tagging data should be made with reference to catch data. Like previous analyses (Hourston 1982), we do not attempt to adjust tag recoveries according to area-specific catch data or fishing rates but acknowledge that this is a required step for further analyses. Further analysis will require that the tagging data be examined in the context of several independent area-specific databases on annual catches, biological samples, and spawn escapement. Detailed cross-referencing and linkages between independent databases was not possible until recent years, with the advent of relational databases and spreadsheets. Even with these new tools, the task is enormous because the databases are large and complex. On the other hand, although further analyses will improve our understanding about biological factors affecting herring fidelity and homing, such further analyses are unlikely to change the basic conclusions of this paper.

In spite of the limitations of these data and analyses, we can make some firm observations and conclusions. First, there appears to be a number of different herring spawning areas in B.C. that have high fidelity rates. Often associated with these areas are differences in spawning times (Hay and McCarter 1997), growth rates, and demographics and populations dynamics (Schweigert et al. 1998). Fidelity rates

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seem to be roughly related to the size of the area under consideration, about 500 km^2 being an approximate minimum size to support high fidelity. In general, results from tagging experiments indicate that there is considerable mixing of individuals among small geographic domains but also show that some herring home to spawning areas used in previous years. An interesting observation is that the geographic scale associated with fidelity rates of 60–80% in Pacific herring in B.C. (~1000 linear km of coastline or a sea surface area of about 4000 km^2) is roughly similar to that described for Atlantic herring in Newfoundland (Wheeler and Winters 1984). From the literature, we note that the genetic status of many herring populations remains uncertain, with few, if any, genetic differences observed over broad geographical ranges (Grant and Utter 1984). We also note that within the ranges for which no apparent genetic differences are described, we may see substantial variation in biology, including variation in spawning times, growth rates, and demographic composition of populations. Further genetic analyses may reveal differences among herring populations. If not, we suggest that the interpopulation mixing (straying and immigration) observed from tagging may be sufficient to preclude neutral genetic differentiation among populations but perhaps not sufficient to prevent local adaptation that results in unique demographics, growth rates, and spawning times.

Acknowledgements

The authors thank Ivan Winther, Dennis Chalmers, Sue Farlinger, and Greg Thomas for their efforts in recovering unpublished anchor-tagging data for inclusion in the herring tagging database. Parts of the paper reflect discussions about fish populations with Chris Wood and others at the Pacific Biological Station. Matt Thompson estimated the sea surface areas of herring sections. The Herring Conservation and Research Society provided the financial support for the work.

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Appendix 1. The number of release sessions per year, sessions with no subsequent tag recoveries, numbers of returned tags, and the recovery rates are shown by year of release. The total return number of 42 767 tags includes some for which recovery information is incomplete.

Year	Release sessions	Releases with no recovery	Number of tags released	Number of tags recovered	Percent recovery
1936	4	0	8 590	53	0.6170
1937	15	0	15 673	955	6.0933
1938	18	0	17 436	469	2.6898
1939	25	2	24 355	1 243	5.1037
1940	29	4	29 502	952	3.2269
1941	21	0	23 870	462	1.9355
1942	19	5	23 209	284	1.2237
1943	13	1	30 131	629	2.0876
1944	15	4	47 374	514	1.0850
1945	16	0	47 579	926	1.9462
1946	18	0	51 531	990	1.9212
1947	22	0	41 551	2 720	6.5462
1948	22	1	45 577	2 630	5.7705
1949	17	0	34 874	1 107	3.1743
1950	29	0	56 435	3 161	5.6011
1951	31	2	69 106	4 044	5.8519
1952	40	1	88 820	1 574	1.7721
1953	53	9	111 693	3 765	3.3708
1954	21	1	42 465	3 057	7.1989
1955	25	9	51 711	1 215	2.3496
1956	28	13	64 978	1 284	1.9761
1957	9	1	28 258	258	0.9130
1958	1	0	10 412	36	0.3458
1959	2	2	7 664	0	10.0000
1964	18	0	33 568	3 771	11.2339
1965	8	0	11 928	1 198	0.0436
1966	4	0	482	29	16.0166
1967	3	3	4 099	0	0.0000
1979	4	0	3 554	33	0.9285
1980	68	23	75 233	147	0.1954
1981	99	30	114 099	783	0.6862
1982	37	3	72 097	625	0.8669
1983	27	6	56 748	243	0.4282
1985	7	1	8 900	76	0.8539
1986	6	0	8 969	300	3.3449
1988	10	0	10 741	280	2.6068
1989	54	7	68 844	602	0.8744
1990	71	8	96 671	1 550	1.6034
1991	46	10	56 522	802	1.4189
All	955	146	1 595 249	42 767	2.6808

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Appendix 2. Monthly summary of numbers and percentages of (*a*) tag releases, (*b*) tag recoveries, and (*c*) tag recoveries from tags at large for one or more years. Numbers of belly and anchor tags are shown separately. The column "Unknown" indicates that the month of recovery was not known.

Tag type (years)		Unknown	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	All
(*a*) **All tag releases**															
All belly tags	*n**	44.8	45.9	66.1	620.1	91.1	4.8	1.8	17.1	35.3	80.2	38.1	17.4	1.4	1 022 871
(1937–1967)	%	4.38	0.45	6.47	60.63	8.91	0.47	0.18	1.67	3.45	7.84	3.73	1.70	0.14	100.00
All anchor tags	*n*														572 378
(1979–1991)	%	0.00	1.00	19.35	51.26	5.20	0.35	0.60	0.00	0.00	3.56	0.00	12.37	6.31	100.00
All tags	*n*														1 595 249
	%	2.81	0.65	11.09	57.26	7.58	0.42	0.33	1.07	2.21	6.31	2.39	5.53	2.35	100.00
(*b*) **All tag recovery**															
All belly tags	*n*	37 026	47	1	1	1	0	0	0	1	0	31	181	37	37 326
(1936–1967)	%	99.20	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.48	0.10	100.00
All anchor tags	*n*	13	96	64	3707	1001	18	18	13	4	6	0	415	86	5 441
(1979–1991)	%	0.24	1.76	1.18	68.13	18.40	0.33	0.33	0.24	0.07	0.11	0.00	7.63	1.58	100.00
All tags	*n*	37 039	143	65	3708	1002	18	18	13	5	6	31	596	123	42 767
	%	86.61	0.33	0.15	8.67	2.34	0.04	0.04	0.03	0.01	0.01	0.07	1.39	0.29	100.00
(*c*) **Tags at large for >1 year**															
All belly tags	*n*	33 309	5	1	1	1	0	0	0	0	0	5	18	28	33 368
(1936–1967)	%	99.82	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.05	0.08	100.00
All anchor tags	*n*	1	2	15	409	28	1	0	1	1	2	0	7	8	475
(1979–1991)	%	0.21	0.42	3.16	86.11	5.89	0.21	0.00	0.21	0.21	0.42	0.00	1.47	1.68	100.00
All tags	*n*	33 310	7	16	410	29	1	0	1	1	2	5	25	36	33 843
	%	98.43	0.02	0.05	1.21	0.09	0.00	0.00	0.00	0.00	0.01	0.01	0.07	0.11	100.00

*All *n* values except those in the final column "All" are × 10^3.

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Herbivory in variable environments: an experimental test of the effects of vertical mixing and *Daphnia* on phytoplankton community structure

Beatrix E. Beisner

Abstract: Phytoplankton communities in lakes are exposed to different within-season frequencies of heterogeneity in resource supply because of wind-induced vertical mixing. Effects of such heterogeneity, in conjunction with herbivory, on phytoplankton community structure have rarely been simultaneously examined, despite the fact that each factor can have large effects on phytoplankton composition and diversity. This study uses replicated oligotrophic mesocosms to examine the effects of herbivory and different scales of temporal heterogeneity in deepwater mixing. The pattern of vertical mixing alone had minor effects on phytoplankton community diversity and composition. The herbivore *Daphnia* caused a shift in phytoplankton composition to less edible types, based mainly on morphological features (spiny shapes and trichomes on cell walls) rather than size structure alone. Phytoplankton richness depended jointly on mixing frequency and large *Daphnia* biomasses. When systems were well mixed, with high encounter rates between predator and prey populations, phytoplankton community richness was lowest. By contrast, the systems that were least often mixed had highest richness. These results are related to limited encounter rates with infrequent mixing and to the availability of refuges from predation. Responses to different scales of temporal heterogeneity in these oligotrophic phytoplankton communities depend more on *Daphnia* feeding than on resource pulsing.

Résumé : Au cours de la saison, le brassage vertical causé par le vent expose les communautés phytoplanctoniques des lacs à des fréquences variables d'hétérogénéité dans l'apport des ressources. Les effets de cette hétérogénéité sur les communautés phytoplanctoniques ont rarement été étudiés en conjonction avec ceux de l'herbivorie, bien que chacun de ces facteurs puisse avoir des effets considérables sur la composition et la diversité du phytoplancton. Nous utilisons dans cette étude des séries appariées de mésocosmes oligotrophes pour examiner les effets de l'herbivorie et de différentes échelles d'hétérogénéité temporelle dans le brassage des eaux profondes. Le régime de brassage vertical seul n'a que peu d'effets sur la diversité et la composition de la communauté phytoplanctonique. L'herbivore *Daphnia* entraîne une prédominance dans la composition du phytoplancton de formes moins facilement comestibles, à cause surtout des caractéristiques morphologiques des cellules (formes épineuses et parois cellulaires ornées de trichomes) plutôt que de leur seule taille. La richesse du phytoplancton varie à la fois avec la fréquence des brassages et la présence de fortes biomasses de *Daphnia*. Lorsque le système est bien brassé et que les taux de rencontre entre les populations de prédateurs et de proies sont élevés, la richesse de la communauté de phytoplancton est à son plus bas. En revanche, les systèmes soumis à un minimum de brassages ont une richesse maximale; cela est dû à un taux de rencontre limité et à l'existence de refuges contre la prédation lorsque les brassages sont rares. Les réactions de ces communautés oligotrophes de phytoplancton à différentes échelles d'hétérogénéité temporelle sont reliées plus à l'alimentation des *Daphnia* qu'à la variation des ressources.

[Traduit par la Rédaction]

Introduction

Equilibrium resource competition theory predicts low diversity for ecological systems in the absence of elaborate niche partitioning. In contrast, natural plankton systems have high diversity, and this is the source of Hutchinson's (1961) "paradox of the plankton." Mechanisms that allow for high diversity in competitive systems include temporal environmental variability, spatial heterogeneity, and predator-mediated coexistence. The interaction of these factors for

Received October 17, 2000. Accepted April 25, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 8, 2001.
J16027

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 DOI: 10.1139/cjfas-58-7-1371 © 2001 NRC Canada

community structure (diversity and composition) remains largely unexplored for phytoplankton.

Role of environmental heterogeneities

Phytoplankton in surface waters are exposed to several sources of temporal and spatial variability in growth factors because of turbulent movement of water that occurs with different frequencies and magnitudes during the growing season. Turbulent vertical mixing events occur as a result of episodic storms, and because these water movements are intermittent, they expose plankton to temporal heterogeneity in ecological conditions that could have consequences for competition. Direct nutrient pulses, change in light and temperature conditions, and eradication of nutrient-depleted patches can result, especially in meso- to eutrophic lakes (Klein and Coste 1984; Harris and Griffiths 1987). Resuspension of bacteria from deeper waters may also provide a pulse of resources with vertical mixing for heterotrophic nanoflagellates, which are common in more oligotrophic systems (Porter et al. 1988).

Based on phytoplankton reproductive rates, Reynolds (1993) characterized ecologically meaningful scales of within-season temporal heterogeneity. High-frequency events should occur every few days (approximately cell generation times), intermediate scales should be on the order of 1–2 weeks, and low-frequency fluctuations should occur less than once every few weeks. Anthropogenic events such as the global climate warming predicted to occur over the next 50 years might change the current pattern of storm events and alter the frequency and intensity of episodic mixing events (Walker 1991).

Past studies of plankton community structure have found large effects on competitive interactions in chemostats exposed to pulses of nutrients across the range of combinations from small-amplitude, frequent fluctuations to infrequent but large pulses (e.g., Robinson and Sandgren 1983; Gaedecke and Sommer 1986; Grover 1991). The applicability of such studies to real lake situations is limited for a number of reasons including a neglect of physical effects other than nutrient pulsing, a focus on enriched systems, an absence of higher trophic levels, use of assembled communities or ones removed from their natural setting, and short temporal and spatial scales. This current experiment aims to address these limitations by using field mesocosms with natural phytoplankton communities exposed to vertical mixing at various frequencies in the presence and absence of the herbivore *Daphnia*.

Role of herbivory

In lakes, the cladoceran zooplankton *Daphnia* spp. is considered the herbivore with the largest impact because of its high grazing rates, generalist foraging strategy, and significant quantitative effects on the success of higher trophic levels and on the structure of phytoplankton communities (Sterner 1989). *Daphnia* can increase phytoplankton community richness (McCauley and Briand 1979), and communities dominated by *Daphnia* have higher grazing rates than those where smaller zooplankton like rotifers are dominant (Leibold 1989). Herbivory by larger zooplankton like *Daphnia* tends to result in high losses for small to midrange, spherical phytoplankton, which allows for the proliferation of larger (>35 μm) types (Porter 1973; Sterner 1989). Whether zooplankton communities are dominated by large *Daphnia* spp. or not can depend heavily on the structure of the fish communities. Through trophic cascades, large *Daphnia* can be far more abundant in systems where piscivorous fish are present and mostly absent from lakes where planktivore populations grow without predators (Soranno et al. 1993).

Interaction of environmental heterogeneity and herbivory

Menge and Sutherland (1987) suggested that the role of predators in regulating prey densities, and therefore the outcome of competition among prey species, can depend on temporal changes in the environment. How intermittent upwelling on various time scales influences phytoplankton community structure in the presence of predators is unknown.

The strength of predator–prey interactions depends on encounter rates (Murdoch and Oaten 1975), which are a function of spatial distributions. In the absence of mixing in lakes, there is potential for natural spatial structure to form in the distribution of phytoplankton owing to local abiotic (i.e., temperature, light) preferences of mobile taxa, differential sinking rates (Reynolds 1992), and patchy distributions of zooplankton (Steele 1978; Threlkeld 1983). Zooplankton patchiness can arise at small scales (<1 m) because of limited mobility and a tendency of zooplankton like *Daphnia* to aggregate in areas of high food density (Levin and Segel 1976; Cuddington and McCauley 1994). Frequent mixing should disrupt the natural spatial structure of both phytoplankton and zooplankton, thereby increasing the encounter rates between different species, especially if patches are generally monospecific. More intense population interactions can lead to greater instability and likelihood of extinctions (Luckinbill 1974; Murdoch and Oaten 1975; McLaughlin and Roughgarden 1991), thereby affecting community composition and diversity. Instability arises because of a lack of spatial and temporal refuges in fully or frequently mixed systems. This study examines the influence of various temporal patterns of intermittent mixing (temporal and spatial heterogeneity), herbivory by *Daphnia*, and the interaction of these factors on phytoplankton community structure in oligotrophic mesocosms.

Methods

The mesocosm experiment consisted of replicate plankton communities isolated and suspended in partly darkened polyethylene bags (~4000 L = 1 m diameter × 5 m deep, open at the surface) in Placid Lake at the Malcolm Knapp Research Forest, southwestern British Columbia, Canada. This montane lake (550 m elevation) is approximately 2.5 ha in area, humic, and oligotrophic (<10 μg total phosphorus·L^{-1}) (Werring 1986). The maximum depth of the lake is 7 m and it is well stratified in the summer with transparency as measured by Secchi depth of 3.5 m. In order to maximize an effect of vertical mixing, the difference between the hypolimnetic and the epilimnetic regions was accentuated by covering the lower 2.5 m of each bag in black plastic. This was done to promote heterotrophic processes over autotrophic ones at depth and promote the recycling of nutrients.

The experimental treatments consisted of two factors with three levels for vertical mixing intervals (5, 15, and 25 days) and two levels for herbivory (presence or absence of *Daphnia*). Time scales were chosen to correspond to both phytoplankton and *Daphnia* generation times and rates of response. The response variable of

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interest with regard to mixing effects is related to the pattern of mixing. Mixing is present in all treatments, with a different pattern of frequency and intensity such that these two factors were inversely related. Thus, the 25-day treatments were mixed for a period of 1 h (moving 2000 L of water), the 15-day treatments were mixed for 36 min (1200 L of water), and the 5-day treatments were mixed for 12 min (400 L of water). This was to ensure that the total mixing associated with each treatment was similar over the longest time scale (i.e., each 25-day period). An unmixed "control" is unwarranted because it represents a pattern of mixing that is unrelated (with a different long-term average) to those applied here. A bilge pump was used to bring water from lower depth (4 m) to the surface. Herbivore treatments consisted of systems with mature *Daphnia rosea* excluded or added. The experiment was run for 75 days from 9 June to 23 August 1997. There were three replicate bags per treatment for a total of 18 bags. A larger number of replicates would increase the power of the test but represent an unmanageable field experiment with a factorial design. The interest here lies in detecting large changes in phytoplankton community structure (i.e., composition, size structure), and as a comparative study, there is an equal power of detection in all treatments.

The bags were filled initially with lake water from several depths, filtered to 54 µm to exclude crustacean zooplankton. The bags were filled on 13 and 14 May 1997. Over a period of 2 weeks (22 May to 3 June), *D. rosea* at a total of 1.2 individuals·L^{-1} were inoculated into half the bags to provide the *+Daphnia* treatment. *Daphnia* were collected by gentle vertical tows in the lake with a plankton net and were separated by handpicking from other zooplankton before inoculation at lake densities into the appropriate bags.

Unfortunately, all non-*Daphnia* mesocosms in this study were subject to a small invasion of *Daphnia* by the midpoint of the experiment (i.e., starting on approximately 27 July in all). Nevertheless, there were still large enough differences between the treatments to allow for meaningful comparisons. First, there were 40 days during which no *Daphnia* were present and treatment comparisons can therefore be made on the basis of whether *Daphnia* were initially present. Second, even though *Daphnia* invaded, the population size structure in the two cases differed radically. Systems that had *Daphnia* stocked initially were composed of very large, adult individuals, while those undergoing invasion consisted of small populations of juvenile *Daphnia* during the time period for which phytoplankton counts were done. During the period for which phytoplankton counts were done (latter half of the experiment), average *Daphnia* biomass was 10.2 µg·L dry weight^{-1} (density of 2.7 individuals·L^{-1}) in treatments where the herbivore had been added and 6.06 µg·L dry weight^{-1} (density of 2.2 individuals·L^{-1}) in treatments where they had been initially excluded. Smaller zooplankton in general consume lower quantities of phytoplankton over a smaller size range (Leibold 1989). For these reasons, the treatments will continue to be referred to as initially planned, as either *+Daphnia* or *–Daphnia*. Because of the invasion, the experiment actually represents a conservative test of the effects of herbivore feeding. Thus, changes in phytoplankton community structure related to the herbivore effect are likely to be strong responses.

Sampling

Phytoplankton were sampled on the third day following a mixing event and every 5 days thereafter at two depths (1.5 and 4 m from the surface) using a 2-L Van Dorn bottle. A 250-mL sample was preserved immediately using several drops of Lugol's iodine. In the laboratory, phytoplankton were counted over a full 25-day cycle during the warmest period of the summer (24 July to 23 August) when the lake was maximally stratified. Enumeration and measurements of cell size and shape were done using an inverted microscope and 50 mL of preserved sample that had settled for 20 h. Transects were counted at 400× magnification until at least 100 cells of the most common group had been enumerated. Phytoplankton were identified to genus except for small unidentified flagellates (<3 µm maximum linear dimension), which were counted as one group.

Daphnia were sampled midmorning, after phytoplankton sampling was complete at the same two depths. Using a bilge pump, 25 L of water was pumped and filtered through a 64-µm-mesh net. *Daphnia* were anaesthetized with soda water and preserved in 4% sugared formalin. Entire samples were counted using a dissecting microscope and conversions to biomass were done using a published length – dry weight relationship for similarly sized *Daphnia longispina* (Bottrell et al. 1976).

Nutrient samples for soluble reactive phosphate were taken from one replicate per treatment prior to and just after mixing events on 4 July and 23 August. The water samples were filtered using a combusted GF/F filter and the filtrate was frozen until later analysis with an autoanalyzer.

In 1999, in situ video measurements of *Daphnia* distributions were done inside an extra bag setup with phytoplankton and *Daphnia*. A camera with a field of view of 7 × 7 × 1 cm was lowered to 1.5 m from the surface of the water. Video footage of *Daphnia* individuals was shot for 30 min before mixing, during a 5-day mixing event, and for another 30 min postmixing. For analysis, *Daphnia* positions from still photographs from 5-min intervals pre- and postmixing were digitized (total of seven photographs premixing and five photographs postmixing). Interneighbor distances were calculated based on Euclidean distances, and from these, an index of dispersion (variance/mean) was calculated for each photograph. The values before and after mixing were compared with a *t* test, with each photograph representing a pseudo-replicate measure.

Data analyses

Relative abundances (RA) of major phytoplankton taxa (phyla) were regressed against time since last mixing (t) for treatments with and without *Daphnia* using the quadratic regression equation

$$RA = y_0 + at + bt^2$$

as this provided the best fit. A factorial repeated measures analysis of variance (RMANOVA) was run on arcsine-transformed time series data to detect whether significant differences owing to treatments depended on time (i.e., whether serial autocorrelation was present).

Average values of relative abundance over the 30-day period for which samples were counted (24 July to 23 August) were used for further analyses. Unless otherwise indicated (i.e., for analyses of spatial distributions), values were averaged over the two depths.

Several aggregate measures of community structure were calculated. The Shannon diversity index was calculated as

$$H' = -\sum_{i=1}^{S} (p_i)(\log_e p_i)$$

where S is the number of species (richness) and p_i is the proportion of total sample abundance belonging to species i. Evenness was calculated as

$$J' = \frac{H'}{\log_e S}$$

Aggregate community measures (H', S, and J') were compared in two-way analysis of variance (ANOVA) with herbivory (two levels) and mixing frequency (three levels) as factors. Significant main effects were further analyzed with Tukey's test, and significant interactions were explored using orthogonal contrasts.

For the statistical analyses, relative abundances of phytoplankton taxa were combined into descriptor classes based on as-

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pects of (*i*) size (four classes: <5, 6–20, 21–35, and >35 μm), (*ii*) morphological features (six classes: round, long, filamentous, spiny, hairy or long flagella present, and amorphous), and (*iii*) mobility (four classes: solitary nonflagellates, solitary flagellates, colonial nonflagellates, and colonial flagellates). Taxa encountered and classification into these various groups are given elsewhere (Beisner 2000; B.E. Beisner, unpublished data). These community composition variables were used as multivariate descriptors of each community type in each treatment. Communities were defined by one descriptor class vector at a time, and a factorial multivariate analysis of variance (MANOVA) was run on each to determine whether there were treatment effects. Thus, a total of three MANOVAs were run and significance was determined by Wilks' λ. A stepwise discriminant analysis indicated which groups in each descriptor class contributed most to main effect treatment differences. It turned out, however, that most significant effects in the MANOVA were interactions, and for these, contrasts were used to determine where differences occurred (i.e., simple effects between treatments). Factorial ANOVAs were done on each significant variate describing communities to determine where the significant interactions lay. In addition, in order to determine which species were producing the observed patterns at higher levels of resolution (i.e., aggregate community descriptors), ANOVAs were run on the relative abundances of common species (>1% of total density) to determine main and interaction effects of the applied treatments.

To assess vertical spatial structure in the distributions of *Daphnia* in the bags, the coefficient of variation (CV) between the shallow and deep samples in each bag was used. Larger coefficients correspond to greater differences between sites in the variables measured, i.e., more spatial heterogeneity.

Results

Physical effects

Mixing events in this experiment did not cause measurable changes in phosphate concentrations. In all cases, soluble reactive phosphate was below detectable levels (<1 $\mu g \cdot L^{-1}$).

Community diversity

For phytoplankton community richness, there was a significant interaction between factors ($P_{interaction}$ = 0.0285) (Fig. 1). When mixing occurred least frequently (25 days), richness was highest with *Daphnia* (P = 0.0474). An opposite trend was found when mixing occurred frequently (5 days). Here, richness was slightly less with *Daphnia* (P = 0.0614). At intermediate mixing frequencies (15 days), there was no effect of *Daphnia* on richness levels. Only with *Daphnia* was richness significantly higher for the 25-day mixing regime than for the 5-day mixing (P = 0.0095). Without the herbivore, there was no significant effect of mixing schedule on richness (P > 0.05) (Fig. 1).

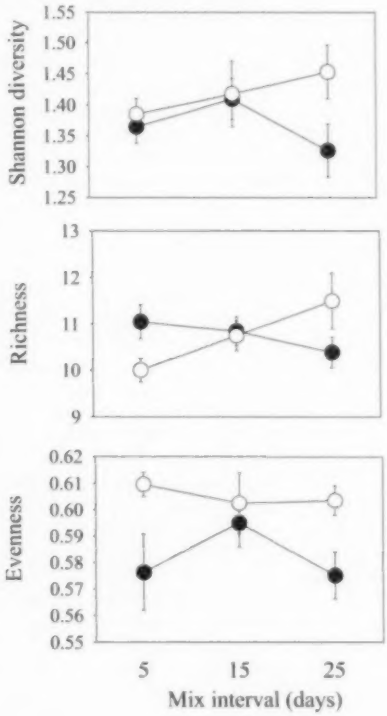
Phytoplankton species diversity was not significantly affected by the treatments (Fig. 1). Evenness was similarly unaffected (Fig. 1) except for a main effect of *Daphnia*. *Daphnia* significantly increased the evenness of phytoplankton communities (P = 0.03; +*Daphnia* (mean ± 1 SE) = 0.61 ± 0.006 (n = 3), –*Daphnia* = 0.58 ± 0.009).

Community composition

Time series

The relative abundances of major taxa (phyla) as a function of time since mixing (Fig. 2) show that the dominant groups at all time periods were chlorophytes and chrysophytes regardless of whether *Daphnia* were initially present or not. Cryptophytes and pyrrhophytes (dinoflagellates) appear to do well just after a mixing event in the presence of *Daphnia* and in their absence, respectively. However, a RMANOVA showed that these trends over time were not significant. The factorial RMANOVA on the time series showed no significant interaction of time with the other treatment factors (mixing and *Daphnia*) (all P > 0.05). The lack of statistical trend with time led to the use of a time average of relative abundances in further analyses.

Fig. 1. Interaction effects of levels of *Daphnia* and mixing frequency on measures of phytoplankton community diversity (mean ± SE). Solid circles represent –*Daphnia* treatments and open circles represent +*Daphnia* treatments.



Size classes

The MANOVA revealed significant main effects of both mixing frequency (MANOVA, P = 0.0205, Wilks' λ = 0.17) and *Daphnia* presence (Table 1) on the phytoplankton communities but no significant interaction. A discriminant analysis on these main effects showed that the mixing effect was mainly due to changes in the 6–20 μm class, which had lowest relative abundances in the intermediate (15-day) treatments (MANOVA, P = 0.016, Wilks' λ = 0.58). For the *Daphnia* effect, the main groups leading to differences based on the discriminant analysis were the 21–35 and >35 μm classes (Table 1). Both of these larger size classes were relatively more abundant with *Daphnia*.

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Fig. 2. Relative abundances of phytoplankton phyla as a function of time since the last mixing event for *+Daphnia* and *–Daphnia* treatments. Solid lines represent the quadratic regression fit for the *+Daphnia* treatments (data are triangles) and dashed lines represent the regressions for the *–Daphnia* treatments (data are circles).

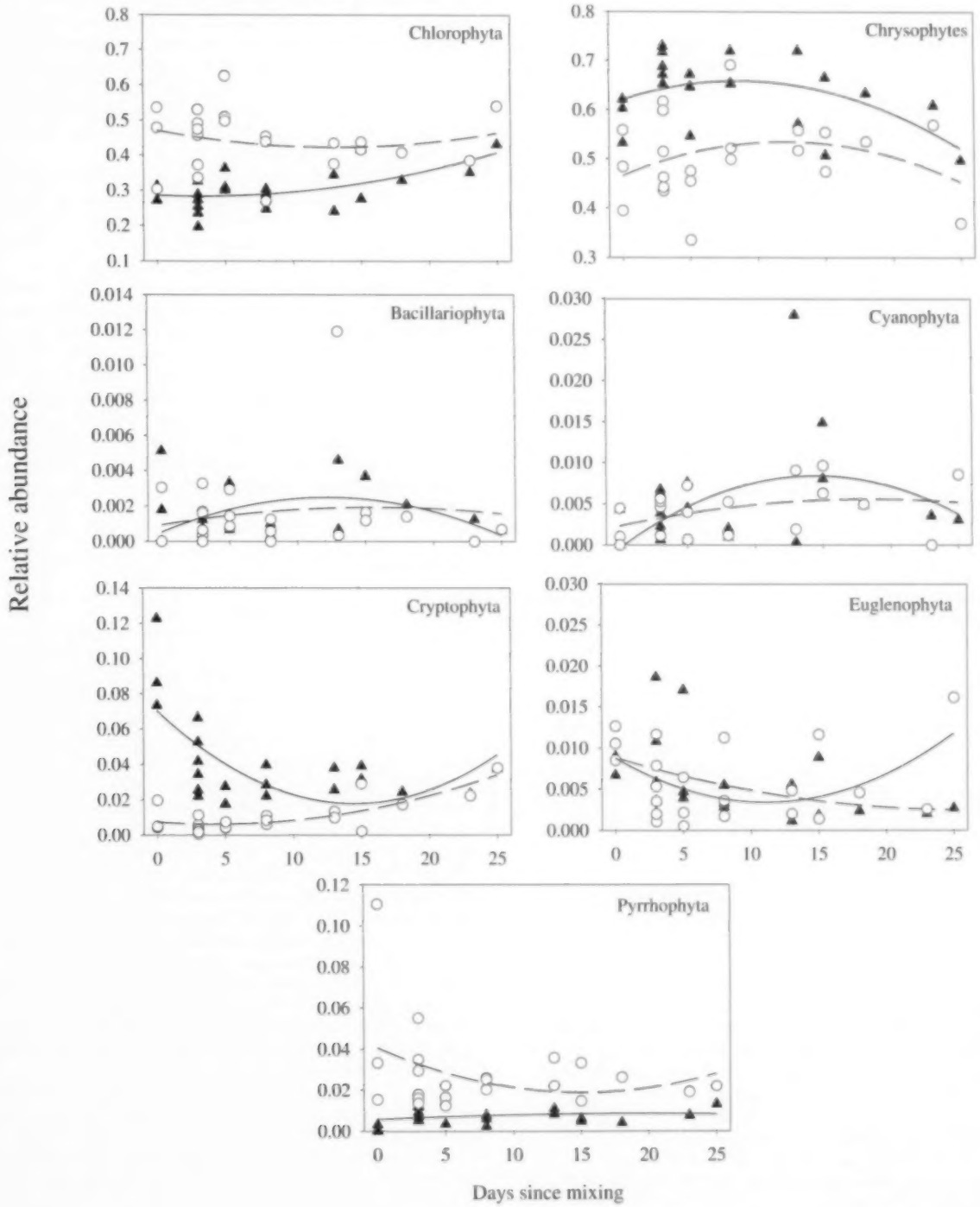

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Table 1. *P* values and Wilks' λ values for the main effect of *Daphnia* in the two-way MANOVAs.

Group	*P*	λ
Size classes (μm)		
MANOVA	0.0002	0.11
<5	ns	ns
6–20	ns	ns
21–35	0.0001	0.38
>35	0.0001	0.27
Morphological features		
MANOVA	0.0252	0.19
Round	0.0005	0.46
Long	ns	ns
Filamentous	ns	ns
Spiny	ns	ns
Hairy, large flagella	ns	ns
Amorphous	ns	ns
Mobility classes		
MANOVA	0.0003	0.11
Solitary nonflagellates	0.0001	0.22
Solitary flagellates	ns	ns
Colonial nonflagellates	0.0001	0.34
Colonial flagellates	ns	ns

Note: Values for the groups within each class are based on the stepwise discriminant analysis. ns, not significant.

Morphological features

The MANOVA based on vectors of morphological features showed only a significant effect of *Daphnia* presence (Table 1). The discriminant analysis revealed that this was due to a decline in the "round" group with *Daphnia*.

Mobility classes

The only significant difference in the case of the vector defined by mobility class was for the effect of *Daphnia* (Table 1). The important groups leading to this main effect were the solitary nonflagellates and the colonial nonflagellates. The solitary types were more abundant with *Daphnia*, while the colonial types had lower abundances when the herbivore was present.

Species composition

The relative abundance of *Chlamydomonas* and nanoflagellates showed a main effect of mixing frequency in univariate ANOVAs ($P = 0.03$) (Fig. 3*a*). *Chlamydomonas* were relatively more abundant in infrequently mixed systems (25 days); the nanoflagellates also did better with less frequent mixing (15 and 25 days) ($P = 0.02$).

The *Daphnia* treatments had effects on the relative abundances of more individual species than did mixing (Fig. 3*b*). *Daphnia* significantly reduced the abundances of *Chlamydomonas* ($P = 0.0003$), nonmotile chlorococcales ($P = 0.0001$), *Gymnodinium* ($P = 0.0001$), and *Oocystis* ($P = 0.0001$). Species that did proportionately better with *Daphnia* were *Ankistrodesmus* sp. ($P = 0.0001$), *Cryptomonas erosa* ($P = 0.0003$), *Mallomonas* sp. ($P = 0.0036$), and nanoflagellates ($P = 0.003$).

Assessing spatial heterogeneity

To examine the short-term effect of physical mixing on large-scale *Daphnia* distributions, the variation between shallow and deep samples was measured in one replicate immediately before and after mixing in the 5- and 25-day treatments on a single date. Before mixing, CVs were 59 in both measured bags. Mixing reduced the variation between the two spatial locations in both treatments, which suggests that the mixing process redistributed *Daphnia* more evenly. The reduction of the CV induced by the longer 25-day mixing treatment was greater (postmixing CV of 49.6) than the reduction in the shorter mixing done in the 5-day treatments (postmixing CV of 38.2).

Video analysis for small-scale (temporal and spatial) effects of mixing indicated that the distribution of *Daphnia* was more clumped prior to mixing. The index of dispersion (CV of nearest neighbor distances) was 12.2 ± 1.2 before mixing and 6.8 ± 0.7 after mixing (*t* test, $P = 0.005$).

Finally, phytoplankton community richness was assessed as a function of the spatial variation (CVs) in *Daphnia* distributions (large temporal and spatial scales). Over the time period during which phytoplankton counts were done, the CVs for the two depths were calculated for the +*Daphnia* treatments. A weak correlation ($P = 0.09$, $r = 0.21$) between richness (square root transformed) and this arcsine-transformed variable was observed (Fig. 4), which only suggests at a trend for phytoplankton community richness to increase with greater spatial variability (CV) in *Daphnia* vertical distributions.

Discussion

Environmental heterogeneity

Community-level attributes of diversity, richness, and evenness were not affected by the frequency of mixing alone. The only significant effect was a minor one on the size structure of the communities. Previous work had demonstrated that phytoplankton diversity can be strongly influenced by mixing (e.g., Reynolds et al. 1983; Lindenschmidt and Chorus 1998), and this has been related to the effects of nutrient pulsing (e.g., Robinson and Sandgren 1983; Gaedecke and Sommer 1986; Grover 1991) and light regime shifts (Huisman et al. 1999). The lack of effect here is surprising but may be attributed to two factors: low between-species contact rates on large spatial scales and low nutrient levels. Full mixing in chemostats results in high contact rates between species. More intense interactions that result should lead to a greater potential for change, since strong species interactions can destabilize communities (Murdoch and Oaten 1975; McLaughlin and Roughgarden 1991). Spatial structure afforded by the natural patchiness inherent in plankton distributions acts to stabilize population interactions, thereby making communities more resilient to external changes. In addition, high background nutrient levels may be required to see major changes in phytoplankton community composition with different vertical mixing regimes. Larger nutrient pulses with mixing episodes are provided with enrichment, permitting a greater range of life history types to persist and a greater community response (Beisner 2000; B.E. Beisner, unpublished data).

Herbivore effects

The herbivore *D. rosea* appears to play a stronger structur-

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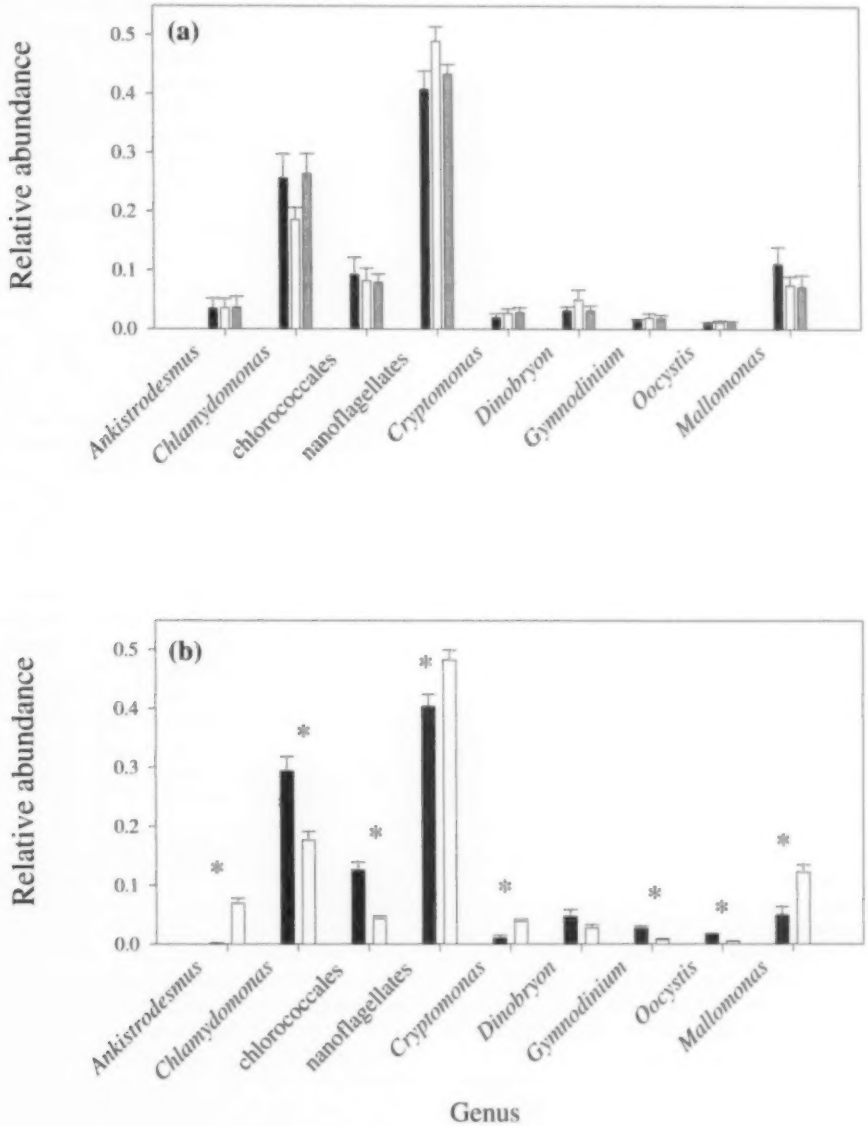
Fig. 3. (*a*) Effect of mixing interval on the relative abundance (mean ± SE) of common taxa (>1% relative abundance). Solid bars represent 5-day mixing, open bars represent 15-day mixing, and gray bars represent 25-day treatments. (*b*) The same for the effect of *Daphnia* on the relative abundances (mean ± SE). Solid bars represent *–Daphnia* treatments and open bars represent *+Daphnia* cases. An asterisk indicates a significant main effect as discussed in the text.



ing role for phytoplankton communities than does mixing frequency. *Daphnia* is a relatively unselective feeder over intermediate size classes of phytoplankton (e.g., Sterner 1989) and increased the evenness of the phytoplankton communities in this study. Given the lack of response of average chlorophyll levels (data not shown) to the herbivore, it is likely that *Daphnia* enhanced evenness by reducing the densities of competitive dominants rather than by simply reducing the population densities of all species.

Examination of the composition of phytoplankton reveals that larger size classes (>20 µm) of phytoplankton were more dominant with *Daphnia*, a result that is consistent with the observation that *Daphnia* feeding is strongest for phytoplankton between 3 and 20 µm (Porter 1973; Sterner 1989). Nanoflagellates (<3 µm) also had higher relative abundances in the presence of *Daphnia*, perhaps because they are relatively inaccessible to the herbivore because of a small body size refuge or because they may be counteracting any effects of predation with very high population growth rates. It has been shown that very small phytoplankton can grow at bacterial rates with several generations per day (Fenchel 1986) and should be able to outgrow zooplankton grazing effects as a result.

Based on morphological features, there was little evidence

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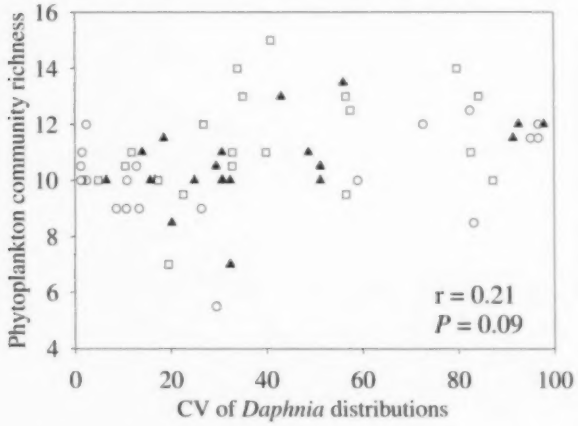
Fig. 4. Correlation of phytoplankton species richness with the CV in the vertical distribution of *Daphnia*. Circles indicate the values for the 5-day mixing treatments, triangles the values for the 15-day treatments, and squares the values for the 25-day treatments. The data shown are for untransformed values.



to indicate differential susceptibilities to filter feeding by *Daphnia*. Only the "round" class responded with higher relative abundances when *Daphnia* were initially excluded. This result is likely due to responses of nonmotile chlorococcales, which had lower relative abundances in the presence of *Daphnia*. Morphology may have also driven the responses of several genera that showed "resistance" to *Daphnia* consumption. Univariate comparisons showed responses in *Ankistrodesmus*, *Mallomonas*, and *Cryptomonas*. *Ankistrodesmus* may be less edible to the moderately sized *D. rosea* because of its sharply pointed crescent shape, despite being edible to the larger *Daphnia pulex* (Lynch and Shapiro 1981). Similarly, *Mallomonas* may be less edible and preferred because of bristles on the cell wall (Lehman and Sandgren 1985). Finally, *Cryptomonas* may use its large flagella and strong swimming ability to escape predation.

Solitary nonflagellates appear to be the most responsive mobility class to *Daphnia* grazing. We might naively expect this group to be most susceptible to grazing by *Daphnia* because of the lack of mobility and the simpler structure of each edible unit. An avoidance of *Ankistrodesmus* and *Mallomonas* is likely responsible for this unexpected response. The response of colonial nonflagellates with lower relative abundances in the presence of *Daphnia* is primarily due to the response of *Oocystis*, a small colony within the size class that *Daphnia* prefers without protective morphological features.

Interaction of mixing and herbivory

The major question of interest here is whether strong herbivory and the scale of episodic mixing interact to influence phytoplankton communities. Turbulent mixing has been shown to alter zooplankton distributions and increase encounter rates with phytoplankton (Haury et al. 1990; Browman 1996). In strongly linked predator–prey systems such as the *Daphnia*–phytoplankton one, increasing encounter rates between species or decreasing the availability of refuges in time or space can decrease population stability (Luckinbill 1974; Murdoch and Oaten 1975) and consequently species richness (Caswell 1978; Hixon and Menge 1991).

For a predominantly competitive process (cases where *Daphnia* were absent), the results here suggest that the pattern of mixing has little effect on phytoplankton community structure. Frequent disruption of natural distributions of phytoplankton probably has minor effects because of the extremely low nutrient levels throughout the oligotrophic systems and the high mobilities of most cells here (i.e., ~90% flagellates). Spatial segregation through vertical layering and patchiness at the scale of these enclosures alone do not seem to be major mechanisms for maintaining diversity.

For the predator–prey systems (i.e., when *Daphnia* were included), the scale of episodic mixing did affect community richness. More frequent mixing lowered prey species richness, while infrequent mixing led to higher levels. Several lines of evidence support the idea that frequent mixing altered encounter rates between predators and prey, reducing the availability of refuges and prey community richness. The weak correlation of phytoplankton richness with the spatial disparity (CV) of *Daphnia* densities suggests that the number of prey genera present is positively related to the degree of or patchiness in *Daphnia* distributions. The reduction in the discrepancy (CV) between the *Daphnia* density samples taken at two depths immediately following a mixing event suggests that *Daphnia* were distributed patchily prior to mixing on large spatial (mesocosm-level) scales and that mixing reduced this heterogeneity. The video measurements indicate that even on very small (centimetre) scales, *Daphnia* distributions become less patchy following imposed mixing. Taken together, these results indicate that mixing destroys the natural patch structure of predators and prey.

The pattern of episodic vertical mixing can affect phytoplankton community structure in oligotrophic systems but not when strong herbivory by *Daphnia* is excluded. The structuring role of mixing appears to operate by changing the encounter rates between predators and prey. It is through this indirect pathway that environmental forcing influences phytoplankton community structure here. This result is different from pulsed nutrient laboratory studies, in part because the study system here is oligotrophic and not fully mixed. However, mesocosms also represent an abstraction of reality (i.e., a lake) that is incomplete. Mesocosms are subject to periphyton growth, although that was a negligible effect here because the systems were of such low productivity. Artifactual results can arise with mesocosms as well as with chemostats, but they do represent one step closer to providing understanding of processes occurring at the lake scale.

This study has shown, through the use of larger oligotrophic systems with additional trophic levels, that relevant life history characteristics for responses to mixing are not just those associated with nutrient uptake abilities because the range of abilities in such a community, adapted to low nutrient conditions, is necessarily small. We might expect larger responses in more enriched systems because a greater range of morphologies and life histories of phytoplankton can persist. Size-structured interactions with *Daphnia* may be more important when larger, filamentous phytoplankton are more common. Responses to the pattern of mixing may also be greater where nutrient pulses are larger. For this

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oligotrophic system, however, the interaction of predation by *Daphnia* (top-down force) with vertical mixing appears to be more important than the interaction with nutrient acquisition (bottom-up force).

Acknowledgments

Thanks to W.E. Neill, C.J. Walters, P.J. Harrison, S.R. Carpenter, and J.P. Grover for comments on earlier drafts. K. Kerr and D. Dolecki provided valuable field assistance and S. Hinch and P. Rand provided video equipment. This research was funded by a Natural Sciences and Engineering Research Council of Canada operating grant to W.E. Neill and by University of British Columbia graduate and Killam predoctoral fellowships to the author.

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Early familiarity has fitness consequences for Arctic char (*Salvelinus alpinus*) juveniles

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Abstract: Familiarity is an important factor reducing aggressiveness among individuals. Because of the reduced energy and time expenditure due to lowered aggression, individuals would be expected to perform better in groups of familiar conspecifics as compared with individuals in groups of strangers. However, few studies have examined potential fitness consequences of familiarity. We created familiar (from tanks where several thousands of unrelated fish had been kept since fertilization) and unfamiliar (by combining fish from several tanks) groups of underyearling Arctic char (*Salvelinus alpinus*) and followed their performance for a 21-day period. Familiarity within groups enhanced survival and body condition of the fish. The fish in familiar groups also grew better in weight and in length. Furthermore, familiar fish differed less in length variation after the experimental period compared with fish reared in unfamiliar groups. There was also a tendency towards similar difference in the variation of weight. These results provide direct evidence for beneficial fitness consequences of early familiarity in Arctic char.

Résumé : La familiarité est un facteur important de réduction de l'agressivité entre les individus. À cause de la diminution des dépenses d'énergie et de temps due au déclin de l'agressivité, les individus devraient fonctionner mieux parmi des groupes conspécifiques familiers que parmi des groupes d'étrangers. Peu d'études ont cependant examiné les conséquences potentielles de la familiarité sur le fitness. Nous avons créé des groupes d'Ombles chevaliers (*Salvelinus alpinus*) de moins de 1 an, familiers (en gardant depuis leur fécondation des milliers de poissons non apparentés dans des aquariums) et non familiers (en mélangeant des poissons de plusieurs aquariums) et nous avons suivi leur performance pendant 21 jours. La familiarité à l'intérieur du groupe augmentait la survie et la condition des poissons; la croissance en masse et en taille était améliorée. De plus, à la fin de l'expérience, les poissons familiers affichaient moins de variation dans leurs tailles que les poissons non familiers; les variations de masses suivaient la même tendance. Il s'agit donc d'une preuve directe des conséquences bénéfiques sur le fitness d'une familiarité à un âge précoce chez les Ombles chevaliers.

[Traduit par la Rédaction]

Introduction

The ability of animals to recognize each other plays an important role in a variety of social relationships ranging from cooperation (Dugatkin 1997) to agonistic interactions among individuals (Walls and Roudebush 1991; Waas and Colgan 1994). The level of discrimination may vary from that of species and populations (Brown and Colgan 1986; Courtenay et al. 1997) to discrimination among specific individuals or types of individuals (Dugatkin and Sih 1995).

Members of a number of fish species seem to discriminate conspecifics on the basis of prior experience with them (Dugatkin and Alfieri 1991; Metcalfe and Thomson 1995; O'Connor et al. 2000) and often show preference for familiar conspecifics as opposed to unfamiliar ones (e.g., Brown and Smith 1994; Magurran et al. 1994; Barber and Ruxton 2000). In recent studies, familiarity has been shown to lower aggressiveness in swordtails (*Xiphophorus nigrensis* and *X. multilineatus*) (Morris et al. 1995), rainbow trout (*Oncorhynchus mykiss*) (Johnsson 1997; Johnsson and Åkerman 1998), Atlantic salmon (*Salmo salar*) (O'Connor et al. 2000), and threespine stickleback (*Gasterosteus aculeatus*) (Utne-Palm and Hart 2000), although in some cases the results have not been so clear-cut, being largely dependent on the dominance relationships of the individuals (Johnsson 1997; Johnsson and Åkerman 1998; O'Connor et al. 2000).

Received September 14, 2000. Accepted April 17, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 12, 2001.
J15973

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 DOI: 10.1139/cjfas-58-7-1380 © 2001 NRC Canada

Evidence has also been found for more stable dominance hierarchy, increased food intake, and better utilization of food as a consequence of familiarity within a group (brown (sea) trout (*Salmo trutta*)) (Höjesjö et al. 1998).

The above studies together suggest that discrimination by familiarity may have fitness value. Consequently, if interactions among familiar and unfamiliar individuals are to be of importance, they should be directly measurable in fitness-related characters. Indeed, benefits of familiarity have been demonstrated in reproductive success in mammals (König 1994) and in birds (Beletsky and Orians 1989). For fish, body size is a character correlating with fitness, as it may often determine their survival probabilities and fecundity, larger and faster growing individuals generally having the advantage over their smaller conspecifics (Kamler 1992; Wootton 1998). The three studies that, to our knowledge, have investigated the fitness effects of familiarity in fish thus far have, however, yielded inconsistent results. In dyadic contests between individual rainbow trout, Johnsson (1997) did not find familiarity with an opponent to improve an individual's growth rate, while Johnsson and Åkerman's (1998) results suggested possible benefits of familiarity for the loser but costs for the winner of the contest in terms of growth. Finally, in Höjesjö et al.'s (1998) study with groups of six sea trout, 8 days in an experimental tank with the same individuals resulted in wild trout losing less weight than when half of the fish were changed for the last 3 days of the experiment. However, such an effect of familiarity was not observed in the growth of the sea-ranched trout. All three studies were rather short in duration (5–8 days), and it may not be surprising that significant differences were not always found.

In the aforementioned studies with salmonids, recognition of specific individuals was presumably underlying the observed responses to familiarity. However, there is evidence that discrimination can also occur without direct individual recognition taking place, but rather, it may be influenced by prior physical and (or) chemical contact with a group of conspecifics. In other words, individuals may learn some group-specific, often chemical, cue they will use as a basis for later discrimination (Hepper 1986). Most of the work examining, and finding, such discrimination in several salmonid species has been conducted on kin recognition. Attraction towards siblings was reported in coho salmon (*Oncorhynchus kisutsch*) (Quinn and Busack 1985; Quinn and Hara 1986), Arctic char (*Salvelinus alpinus*) (Olsén 1989; Winberg and Olsén 1992; Olsén and Winberg 1996), and Atlantic salmon and rainbow trout (Brown and Brown 1992, 1993*a*; Brown et al. 1993). Furthermore, lowered aggressiveness and (or) higher growth in kin groups was found in Atlantic salmon and rainbow trout (Brown and Brown 1993*a*, 1993*b*), brown trout (Olsén et al. 1996), and Arctic char (Brown et al. 1996; Olsén and Järvi 1997). In two studies, the preference for familiar versus unfamiliar sibs was tested (Olsén 1989; Brown et al. 1993), but none of the studies considered whether familiarity itself (early exposure to nonkin versus no experience of nonkin) might promote discrimination. Recently, the fry of some coho salmon families were found to prefer chemical cues from a group of unrelated conspecifics whom they had been chemically exposed to during the early life phases (alevin and free-swimming fry stage) over cues from unrelated, unfamiliar fish (Courtenay et al. 2001). No study has examined possible fitness consequences of such discrimination.

In this paper, we investigate the role of familiarity in the performance of Arctic char fry. We explore whether early experience in a rearing group (i.e., familiarity) affects growth, condition, and survival of the fry. Social behaviour in juvenile Arctic char ranges from territoriality with aggressive interactions (Noakes 1980) to schooling behaviour (Klemetsen and Grotnes 1980). Under both of these conditions, familiarity could diminish the costs involved in competing for resources. Individuals would therefore be expected to grow faster and thus attain a larger size in groups of familiar individuals than in groups of strangers. They would also be expected to show less variation in growth and thus in final size in familiar groups. Furthermore, condition and survival should be enhanced in groups of familiar individuals.

Methods

Fish maintenance

The experiment was conducted in June–July 1997 at the facilities of Saimaa Fisheries Research and Aquaculture in Enonkoski, eastern Finland. The study fish were second-generation hatchery young-of-the-year Arctic char derived from a landlocked strain native to Lake Saimaa.

To create the fish groups that were later used as the source for the experimental groups, thousands of eggs from several pairs of females and males were combined immediately after fertilization and incubated in seven separate standard hatchery troughs, each containing eggs from a different set of parental pairs. Due to the standard hatchery practices, the number of parental pairs, i.e., families, per trough varied from 49 to 134, except one trough with only 18 families. In the last mentioned trough, the eggs of each female were divided into two equally sized batches and fertilized with the milt of two males, while in all of the other troughs, the eggs of each female were fertilized with the milt of a different male, each female and male being used only once in the fertilizations. After the start of exogenous feeding, the fish were moved from each trough to a separate circular tank (diameter = 200 cm, $N = 7$), where they were maintained in standard hatchery conditions for approximately 1 month prior to the start of the experiment. There was a separate water inlet for each trough and tank, and the water was not recirculated before or during the experiment.

Experimental procedure

In the experiment, we used circular plastic tanks (diameter = 50 cm, height = 43 cm) with a tap in the periphery and a central drain. The water level in each tank was 15 cm and the flow rates were kept constant at 1.5 times fish length per second. The water temperature ranged from +8 to +10°C following the ambient temperature of a nearby lake where the water to the hatchery is taken from. To minimize disturbance, each tank had a lid, which remained closed except during cleaning every other day when dead fish were also removed. The fish were hand fed in excess four times a day through a mesh in the lid. The mesh also allowed light to pass into the tanks. Food ration was 4% of the biomass in the tanks per day. After 10 days, the amount of food was tripled to ensure excess feeding for the latter part of the experiment. The lighting was uniform and moderate by overhead fluorescent bulbs following a 16 h light : 8 h dark cycle.

We used 17 experimental tanks with 50 fish in each as well as seven replicate tanks for familiar groups and 10 replicate tanks for unfamiliar groups. The unfamiliar groups were formed by randomly taking seven or eight fish from each of the seven source

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Table 1. Tank mean (SE) weights, lengths, condition (residuals from a log(length) – log(weight) regression), and CVs of weight and length for familiar and unfamiliar Arctic char at the beginning of the experiment.

	Weight (g)	Length (mm)	Condition	CV weight	CV length
Familiar	0.60 (0.05)	44.6 (1.09)	0.15 (0.13)	18.9 (1.50)	5.69 (0.46)
Unfamiliar	0.53 (0.03)	43.0 (0.65)	–0.02 (0.06)	23.7 (0.93)	7.24 (0.30)

Fig. 1. Mean mortality of Arctic char in familiar and unfamiliar groups. The lines above the bars represent standard errors.

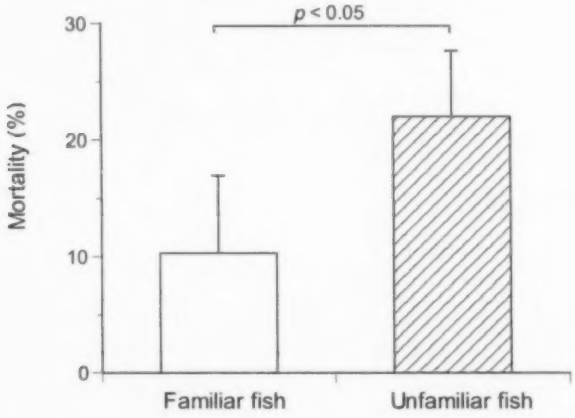
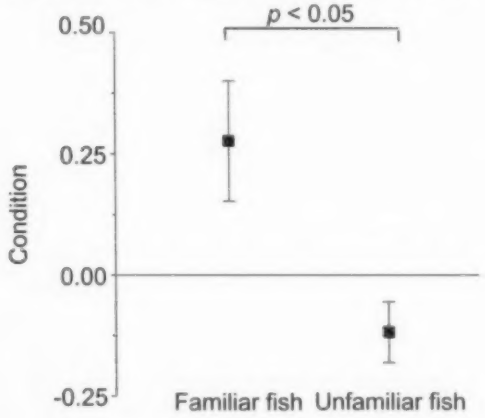


Fig. 2. log(length) – log(weight) regression model residuals (tank means ± SE) for the groups of familiar and unfamiliar Arctic char.



tanks available and placing them together in an experimental tank. A random sample of 50 fish from each source tank created the familiar groups. Hence, our design does not absolutely rule out the possibility that some fish, especially in the familiar treatment, are related to each other. However, considering the large number of parents in each source tank (see above), the number of closely related fish per experimental tank is likely to be very low.

At the start of the experiment, the fish were lightly anaesthetized with MS 222 (2.5 mL·L^{-1}) and the weights and lengths of all fish were measured. The weights of the fish at the beginning of the experiment ranged from 0.2 to 1.4 g and the lengths from 34 to 58 mm (Table 1). The experiment was terminated on day 22 after 21 days of growth. At the end of the experiment, we recorded tank-specific survival and measured body length and weight of each of the surviving fish.

Statistical analysis

Mortality data were arcsine transformed prior to analysis. A two-sample t test was used to test for differences in mortality between familiar and unfamiliar fish. Two-sample t tests were also applied to the data on condition and size of individuals at the end of the experiment using the tank averages as response variables. To avoid potential problems associated with ratio-based condition indices (Reist 1985; Packard and Boardman 1988), we used a condition measure based on standardized residuals obtained from a linear log(length) – log(weight) regression applied to the whole data set. This method has been shown to control well for the confounding effect of initial body size (Jacob et al. 1996). The condition data were not normally distributed, nor were their variances equal. As this was due to only one outlying data point, this data point was left out from the analysis.

We also calculated the coefficients of variation (CVs) for weights and lengths for each tank at the start and end of the experiment to investigate the possible effect of the two treatments on size variation. To test for differences in CVs between familiar and unfamiliar groups, we used an analysis of covariance (ANCOVA), where the average CV for each tank at the beginning of the experiment was used as a covariate to control for the initial differences in the CVs (Table 1). All statistical tests were done using the SYSTAT 8.0 statistical package (Wilkinson 1996).

Results

Juvenile Arctic char survived better in the presence of familiar individuals than in the presence of unfamiliar ones ($t_{15} = -2.19$, $N = 17$, $p = 0.045$), survival being 11.7% higher in the familiar treatment (Fig. 1). Overall, the mortality ranged from 0 to 44% in familiar groups and from 8 to 58% in unfamiliar groups. Also, condition (described as residuals from a log(length) – log(weight) regression) was better in the familiar fish ($t_{14} = 3.09$, $N = 16$, $p = 0.008$) (Fig. 2), fish in the familiar groups being heavier per unit length than fish in the unfamiliar groups. At the beginning of the experiment, there were no statistically significant differences in body condition between the treatments ($t_{14} = 1.15$, $N = 16$, $p = 0.180$) (Table 1).

Growth of the fish in both weight and length was affected in a similar way, with groups of familiar individuals growing better than groups of unfamiliar individuals (weight: $t_{15} = 2.17$, $N = 17$, $p = 0.046$; length: $t_{15} = 2.10$, $N = 17$, $p = 0.053$) (Fig. 3). The tank-specific averages of body size at the beginning of the experiment did not differ between the treatments (weight: $t_{15} = 1.29$, $N = 17$, $p = 0.22$; length: $t_{15} = 1.36$, $N = 17$, $p = 0.20$) (Table 1). As differences in stocking densities have been shown to affect growth in Arctic char (e.g., Jobling and Baardvik 1994), we tested whether the differences in mortality between groups of familiar and unfamiliar fish might have influenced our results. The final number of individuals in a group did not correlate with the group mean weight or

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Fig. 3. Mean (*a*) weights and (*b*) lengths of Arctic char in familiar and unfamiliar groups at the end of the experiment. The lines above the bars represent standard errors.

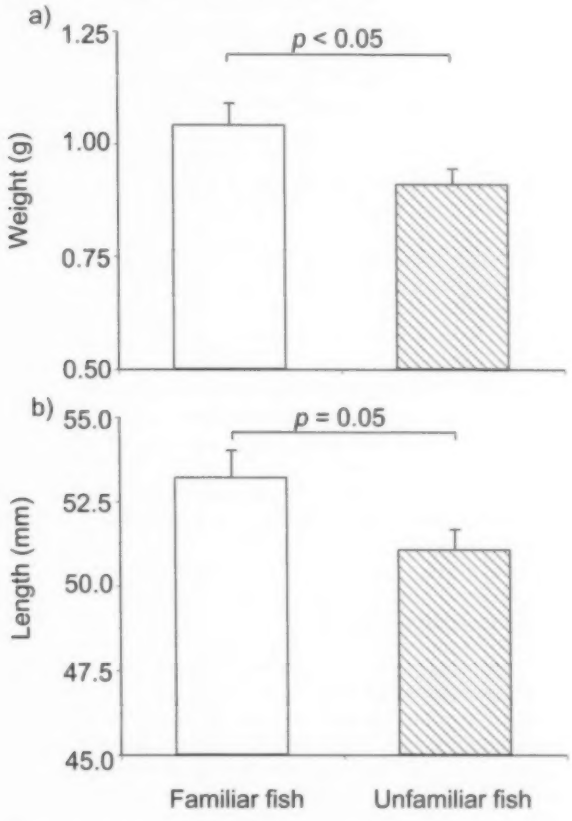
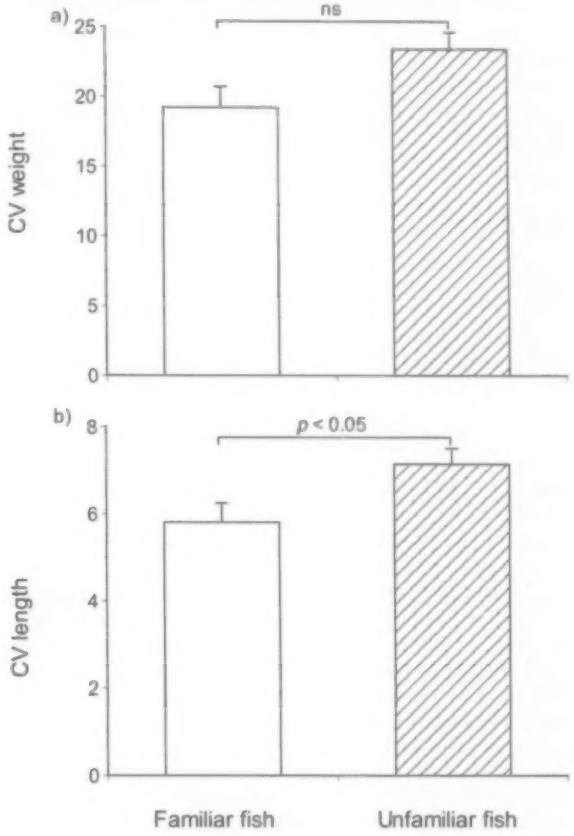


Fig. 4. Adjusted least squared means and standard errors given by ANCOVA for CVs of (*a*) weights and (*b*) lengths of Arctic char in familiar and unfamiliar groups at the end of the experiment.



length (weight: $r_P = 0.171$, $N = 17$, $p = 0.512$; length: $r_P = 0.133$, $N = 17$, $p = 0.611$).

The homogeneity of slopes assumption for ANCOVA was fulfilled for CVs in both weight and length (weight: $F_{1,13} = 0.625$, $p = 0.44$; length: $F_{1,13} = 1.139$, $p = 0.31$), i.e., there was no interaction between the dependent variable and the covariate. The CVs for length were significantly smaller for groups of familiar fish than for groups of unfamiliar fish (ANCOVA: $F_{1,14} = 4.98$, $p = 0.042$) (Fig. 4). There was also a nonsignificant tendency towards smaller CVs of weight in the familiar groups ($F_{1,14} = 3.98$, $p = 0.066$) (Fig. 4).

Discussion

Our results on the performance of Arctic char show that early familiarity among individuals may have important fitness consequences. Firstly, individuals that had been reared together from fertilization survived better than individuals in the groups that were mixed from several groups of fish at the start of the growth experiment. Secondly, the body condition index was lower in the unfamiliar fish, suggesting that individuals in the familiar treatment had a better nutritional status. Thirdly, when examining body size, the fish also grew better when with familiar individuals than when with unfamiliar individuals. Finally, size variation at the end of the experiment was smaller in familiar groups than in unfamiliar groups, this difference being statistically significant in the variation in length.

Recent studies on territorial rainbow trout (Johnsson 1997; Johnsson and Åkerman 1998) and Atlantic salmon (O'Connor et al. 2000) have shown that the rates of aggression may be lower when the fish in experimental groups are familiar with each other. As aggression decreases, so should also the costs of competition (Parker 1974; Maynard Smith and Parker 1976). One such cost could be injury caused by fighting (Abbott and Dill 1985; Neat et al. 1998). Salmonids typically bite each other during a fight (Keenleyside and Yamamoto 1962; Noakes 1980). Although the bite marks are not fatal in themselves, they may increase mortality by making the fish more susceptible to bacterial and fungal infections. It is possible that the greater mortality in the unfamiliar groups of Arctic char may have been mediated by increased susceptibility to infection. Another possible explanation for the increased mortality in the unfamiliar groups would be the spreading of infections as fish from several groups were combined. Nevertheless, none of the source tanks showed signs of infection or increased mortality prior to or during the experiment. Therefore, we do not believe that this could have affected our results.

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Lowered level of aggression is likely to lead to higher food intake rate owing to more time left for feeding. The lowered energy costs as a consequence of a reduction in aggression level (Neat et al. 1998) could also lead to higher utilization of food in the groups of familiar individuals. Although Höjesjö et al. (1998) did not find an overall difference in aggression between familiar and unfamiliar sea trout, their results showed a benefit for the familiar fish in terms of increased food intake and better utilization of food compared with groups of unfamiliar fish. In ectotherms, a reduced rate of food intake or less efficient food utilization may not be a large cost in terms of short-term survival, but the cost may still be manifested in body condition and (or) growth. Our results with Arctic char show that the growth and condition of the fish in familiar groups were better than in the unfamiliar groups. The variation in growth was also smaller in familiar groups, suggesting a more even distribution of resources among individuals. A variety of manipulations that result in lowered aggression among individuals have been shown to lower the variability of growth in Arctic char (Jobling and Baardvik 1994; Brown et al. 1996). Based on these results, we suggest that the costs involved in competing for food resources were lowered in familiar groups of our study.

Our results on growth rates may have been influenced by the length of the growth period in our experiment. Griffiths and Magurran (1997*a*) have shown with schooling guppies (*Poecilia reticulata*) that the preference for familiar individuals develops gradually over 12 days when individuals are kept together in groups of six fish. Johnsson (1997) and Höjesjö et al. (1998) showed effects of familiarity on individual behaviour after only 3 and 5 days of exposure to conspecifics, respectively. Johnsson (1997) used pairs of fish, while in Höjesjö et al.'s (1998) experiment, groups of six fish were used. If the time required to become familiar with others is of similar magnitude for Arctic char, it would have been rather early in our experiment when the fish would have become familiar with each other. However, the results of these studies are not directly comparable with those of our study, where the number of fish in the groups was much larger (initially 50 individuals) and the recognition of specific individuals was thus more unlikely (Griffiths and Magurran 1997*b*). Griffiths and Magurran (1997*b*) showed that the preference to shoal with familiar individuals in guppies was inversely related to group size. The authors suggested that this would be the result of the inability of the fish to individually recognize all of their group mates when the group size was large enough. The time by which individual recognition may develop in groups of Arctic char is not known, nor is its dependency on group size.

Höjesjö et al. (1998) compared the effect of familiarity between wild and sea-ranched sea trout, and although it was expected that the hatchery environment would have selected against individual recognition, their results showed similar effects of familiarity on the behaviour, but not on growth, in both types of fish groups. The fish in our experiment were of hatchery origin and the effect of early familiarity was apparent despite the fact that the fish originated from tanks with several thousand individuals in each. In contrast with Höjesjö et al.'s (1998) study, the recognition of specific individuals is unlikely to play a major role in our system, but instead, chemosensory cues of the types of individuals (familiar, unfamiliar) are more likely.

Spawning Arctic char females dig a nest (redd) in bottom gravel where the eggs are laid, and after hatching, the young stay within the gravel until the start of independent feeding (Fabricius 1953; Johnson 1980). Our results seem to suggest that the common environment during embryonic development or early phases of independent life is sufficient to generate at least some of the benefits that previously have been associated with kin recognition. Interestingly, there is evidence that the preference for kin in Arctic char is modified by early rearing conditions; fish kept in isolation do not prefer the scent of unfamiliar siblings over that of unfamiliar nonsiblings (Winberg and Olsén 1992; Olsén and Winberg 1996). Furthermore, a recent study with guppies has shown familiarity rather than kinship to be more important in individual schooling decisions (Griffiths and Magurran 1999).

Our results clearly show that early familiarity in itself is an important factor affecting growth rates. As the results also show the significance of familiarity on other fitness-related traits, such as condition and survival, quantification of how much kin recognition in Arctic char and other salmonids is dependent on the number of shared genes and how much depends on the familiarity of individuals is an interesting subject for future research.

Acknowledgements

We thank Kai Lindström, Esa Ranta, Lotta Sundström, and three anonymous referees for comments on the earlier drafts of the manuscript. Saimaa Fisheries Research and Aquaculture provided the fish and good working facilities. The Academy of Finland, University of Helsinki, and Finnish Game and Fisheries Research Institute funded this study. This study was conducted with the permission of the Uusimaa provincial board.

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Offshore spawning and year-class strength of northern cod (2J3KL) during the fishing moratorium, 1994–1996

John T. Anderson and George A. Rose

Abstract: Two new surveys have been conducted in recent years to assess the status of the northern cod (*Gadus morhua*) stock (2J3KL). An offshore acoustic survey in spring sampled concentrations of spawning adults and estimated potential fecundity. A pelagic juvenile fish survey carried out in late summer measured cod year-class strength prior to settlement. Spawning biomass of offshore cod decreased from 11 700 t in 1994 to 2000 t in 1995 to 900 t in 1996 with a corresponding decrease in eggs spawned. This decline was mirrored in the distribution and abundance of pelagic juvenile cod. Natural mortality estimated between the egg and pelagic juvenile stages increased from $-0.068 \cdot day^{-1}$ in 1994 to $-0.084 \cdot day^{-1}$ in 1995 to $-0.112 \cdot day^{-1}$ in 1996. The decline in year-class strength of cod appeared to result primarily from a reduction in the number of offshore spawners compounded by an increase in natural mortality during the egg and larval stages. The decline in spawners occurred 2 years after the implementation of a fishing moratorium and cannot be linked to fishing. The rapid decline in abundance of adult fish combined with increased natural mortality during the egg and larval drift is consistent with depensation.

Résumé : Deux nouveaux inventaires ont été menés ces dernières années pour évaluer l'état du stock nordique (2J3KL) de la morue franche (*Gadus morhua*). Un inventaire acoustique au large au printemps a permis d'échantillonner les concentrations des adultes en fraye et d'estimer la fécondité potentielle. Un inventaire des jeunes poissons pélagiques en fin d'été a mesuré la force de la classe d'âge avant l'établissement au fond. La biomasse des géniteurs au large a décru de 11 700 t en 1994 à 2 000 t en 1995 et à 900 t en 1996 et le nombre d'oeufs pondus a baissé en conséquence. Ce déclin s'est reflété dans la répartition et l'abondance des jeunes morues pélagiques. La mortalité naturelle estimée entre le stade oeuf et le stade jeune poisson pélagique a augmenté de $-0{,}068 \cdot jour^{-1}$ en 1994 à $-0{,}084 \cdot jour^{-1}$ en 1995 et à $-0{,}112 \cdot jour^{-1}$ en 1996. La réduction de l'importance des classes d'âges de morue semble être due principalement à une diminution du nombre de géniteurs au large, à laquelle s'ajoute une mortalité naturelle accrue durant les stades embryonnaire et larvaire. Le déclin des géniteurs s'est produit 2 ans après la mise en place d'un moratoire sur la pêche et ne peut donc être relié à la pêche. La diminution rapide de l'abondance des poissons adultes ainsi qu'une mortalité naturelle accrue durant la dérive des oeufs et des larves laissent croire à l'existence d'un effet Allee («depensation»).

[Traduit par la Rédaction]

Introduction

A commercial fishing moratorium was implemented for the northern cod (*Gadus morhua*) stock (NAFO 2J3KL) in July 1992 following a severe decline in abundance (Taggart et al. 1994). In the absence of fishing, marine fish populations are expected to increase in abundance. Predictions based on historical data indicated that the northern cod stock would double in size approximately every 3 years (Myers et al. 1997, modified in Hutchings 1999) or more conservatively every 5–6 years (Hutchings 1999). These predictions were based on an intrinsic rate of natural increase estimated by fitting a Ricker curve to the historical data for this stock. Similarly, Roughgarden and Smith (1996) predicted that the northern cod stock would increase to more than 1.5 million tonnes (t) for the northern cod stock by 1998. Traditional stock assessment methods estimated that the population of cod age 3 and older was 58 million fish in January 1992 (Murphy et al. 1997). This population was dominated by 5- and 6-year-old cod from the 1986 and 1987 year-classes and represented <27 000 t of spawning biomass. Independent estimates from acoustic surveys indicate significantly greater spawning biomass in the spring of 1992 (Rose et al. 2000). Taking the lower biomass estimates, this population should have increased to 75–155 million fish and a spawning biomass of 36 000–72 000 t by 1996 and perhaps twice that if the higher estimate is used. However, the most recent stock assessments indicated that by 1999, the spawning stock biomass has not increased at this rate (Lilly et al. 1999; Shelton and Healey 1999).

Traditional stock assessment methods for the northern cod have largely failed following the collapse of the population. In the absence of a directed commercial fishery since 1992, catch, effort, and age data are no longer available as input into the sequential population models, and analytical models

Received August 15, 2000. Accepted February 16, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 15, 2001.
J15921

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 DOI: 10.1139/cjfas-58-7-1386 © 2001 NRC Canada

have not been accepted since 1993 (Shelton and Lilly 2000). The Department of Fisheries and Oceans carries out offshore bottom trawl surveys annually in the late autumn, based on the assumption that adult cod and juveniles have migrated to overwintering areas on the shelf. Recently, these surveys have not located any adult concentrations offshore (Lilly et al. 1999), confirming that a seasonal migration no longer occurs (Rose 1996). The importance of the inshore areas along the northeast coast of Newfoundland to both adult and juvenile cod has become increasingly evident in the 1990s. Recent studies have demonstrated the coastal region to hold the primary contemporary spawning fish (G.A. Rose, unpublished data) and nursery grounds (Dalley and Anderson 1997*a*; Anderson and Gregory 2000).

Recently, two new research programs were initiated to measure stock performance during the rebuilding period of the northern cod population. An acoustic survey began in June 1994 to measure the abundance of adult and demersal juvenile cod off southern Labrador during the spring postspawning period. The survey is designed to target the historical northern spawning component of the 2J3KL cod stock (Fig. 1). Spawning here has been hypothesized as necessary for successful recruitment with a high probability for retention of eggs and larvae over the shelf (deYoung and Rose 1993). Second, a pelagic trawl survey began in August of 1994 to measure the distribution and abundance of pelagic juvenile cod throughout the coastal and shelf regions of Newfoundland and Labrador following spring spawning (Fig. 1). Historically, pelagic juvenile cod were abundant on the shelf following the period of egg and larval drift (Anderson et al. 1995). Measuring the distribution and abundance of pelagic juvenile cod is designed to give an early measure of recruitment that will relate to the broad-scale spawning distributions of northern cod. It is also an important measure of new production by the stock, before settlement and the prerecruit period of survival when density-dependent processes may significantly alter year-class abundance (Myers and Cadigan 1993; Anderson and Gregory 2000).

Our purpose is to report on the initial findings of these two surveys, 1994–1996, as direct measures of the reproductive output of cod eggs offshore and their subsequent survival as pelagic juveniles. We estimate the total number of eggs produced based on the abundance, maturity, and fecundity of observed spawners and compare this with year-class strength during the pelagic juvenile stage. Abundance of pelagic juvenile cod is a reliable predictor of cod recruitment in most years (e.g., Sundby et al. 1989; Helle et al. 2000). Contrary to predictions based on compensatory-process models (e.g., Ricker 1975), the abundance of the remaining offshore spawning cod declined from 1994 to 1996, with a concomitant decrease in the abundance of pelagic juveniles. This decline was compounded by decreasing survival rates during the egg and larval drift during this same time period. We discuss our findings in the context of cod population dynamics and depensatory mechanisms.

Materials and methods

Demersal cod

An acoustic survey was conducted in the Hawke Channel area in North Atlantic Fisheries Organisation (NAFO) Division 2J in June of 1994–1996 (Fig. 1). A randomly started grid of transects was run over the area with the goal of attaining widespread coverage of the area from approximately 200 to 700 m depth, which brackets the area inhabited by cod in this region. The same grid was run each year, although sampling effort varied somewhat. A total of 1019, 1580, and 947 km of acoustic transects were run in June of 1994, 1995, and 1996, respectively. Transects were run at 8 kn in 1994 employing the vessel *Gadus Atlantica* and in 1995 and 1996 the CCGS *Teleost*. Both are research trawlers modified specifically for acoustic surveying. Echosounders (38 kHz) were calibrated with tungsten carbide and copper spheres according to standard procedures (Foote et al. 1987). In 1994 and 1995, a purpose-built dual-beam system was deployed from a towed body at approximately 100 m depth. In 1995, seven transects were also run with the new hull-mounted EK500 system in the *Teleost* for comparative purposes. Differences in acoustic outputs from the dual- and split-beam systems were not significant (G.A. Rose, unpublished data). Hence, in 1996, the more convenient hull-mounted system was used.

Fishing sets were conducted during each survey to assist signal interpretation and provide biological samples. Sets were targeted at specific "classes" of acoustic signal. All fishing was conducted with the Campelen 1800 research shrimp trawl with small-mesh liner. This net is considered an effective sampling tool for cod age 2 years and older (Godo and Walsh 1992).

Acoustic data were analyzed initially by displaying all transects graphically to identify individual cod signal. Virtually all cod occurred as groups of targets that were readily recognizable from the acoustic record and unlikely to be confused with other acoustic backscatter in that region. During these analyses, fishing data and a library of known acoustic signals were consulted. In virtually all cases, fishing data agreed with independent echogram interpretations. In 1994 and 1995, this process was conducted on older visualization software modified for that purpose. In 1996, the EK500 data was analyzed using FASIT, a new analytical software program designed for visualizing, separating, and quantifying multispecies acoustic signals (LeFeuvre et al. 2000). The major task was to separate cod from shrimp, which were highly abundant in the study region. The analytical strategy was to simultaneously threshold the signal at –75 dB (20 log R) and edit single targets attributable to cod prior to integration. We consider these to be minimal absolute estimates, as no additions were made for cod likely to be present within the bottom zone and undetectable by these echosounders (1–2 m). Hence, the estimates should be considered as minimal and relative with respect to true stock size but absolute in the sense that they are converted by known scaling factors to fish densities. Once the species classification and editing of the bottom and any noise was completed, the remaining cod signal was integrated for each 100 m of distance along all transects.

Cod densities were mapped using MapInfo. The contiguous areas of cod were encircled using a mapping tool and the areas of cod aggregations were estimated. To estimate mean backscatter (s_A) and confidence intervals, a bootstrap method was employed. Acoustic transect data within the aggregations were 25 times resampled at a rate of 2% to reduce autocorrelation in the density data. The 25 means were then used to estimate the 95% confidence intervals, defined as the 2.5 and 97.5 percentiles of the frequency distribution of boostrapped means.

Mean s_A values were scaled to absolute densities using a target strength to length model of TS (dB) = 20 log L (cm) – 67.5 (modified from Rose and Porter 1996; Foote 1987) and detectabilities determined experimentally (Lawson and Rose 1999). Each 4-cm length group was scaled separately as a component of the overall s_A, based on the proportion of each length group in the overall catch. Variance includes sample error and an uncertainty in the assigned target strength of 1 dB. An age to length key based on otolith sampling conducted during this research was used to con-

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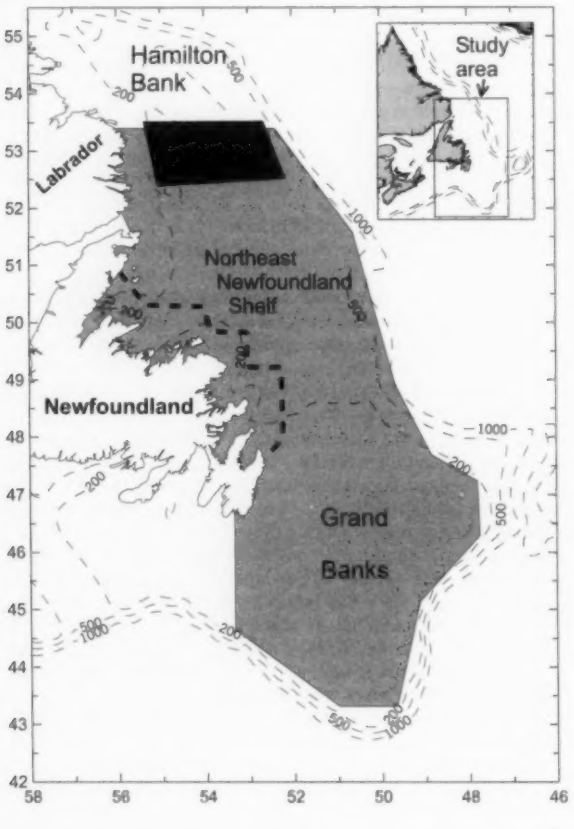
Fig. 1. Northwest Atlantic shelf areas off Newfoundland and Labrador. The shaded area encloses the area surveyed for pelagic juvenile cod in late summer, and the black area is the region surveyed for spawning cod in spring. The heavy broken line demarcates the inshore coastal zone off Newfoundland. Contours are bottom depths (m).



vert length to age to estimate abundance at age. A length to weight conversion based on a model developed from the biological samples was used to estimate biomass.

All cod were fully sampled in 1995 and 1996. In 1994, a random sample of fish caught was fully sampled, and the remainder was measured for length only. Biological measurements included gender, length (centimetres), and whole, gutted, and organ weights (grams). Otoliths were taken and read from all fully sampled fish for ageing. Female gonad condition was categorized as either immature or mature, with mature gonads further divided into three stages according to Morrison (1990). Ripening females had visible opaque eggs. Spawning females had gonads with hydrated eggs, and possibly some eggs already extruded. Spent females had completed spawning and had no, or very few, hydrated eggs. Males were judged to be either immature, ripening (testes enlarged but no visible milt), partially spent (testes enlarged with visible milt), or spent. An estimate of the number of eggs spawned each year was based on the acoustic estimates of abundance in relation to maturity and fecundity at each age, where we assumed a male to female ratio of 50%. Fecundity was estimated from the age–fecundity relationship of May (1967).

Pelagic juvenile cod

Pelagic juvenile fish surveys were carried out in August and September each year, with the middate occurring approximately 2 weeks later in 1995 (Table 1). The survey design is based on a systematic survey grid at a station spacing of 55 km (30 nautical miles). This design is equivalent to a systematic stratified sampling design where the first station was selected randomly from one 55 × 55 km stratum (Snedcor and Cochrane 1967). Within the bays, stations were positioned approximately 55 km apart. The surveys were carried out as a multispecies trawl survey of the plankton and nekton of the northwest Atlantic, as described in Dalley and Anderson (1997*b*).

Table 1. Summary of pelagic juvenile fish surveys conducted during 1994–1996.

Year	Survey dates	DoY	IYGPT stations
1994	22 Aug. – 3 Sept.	234	99
1995	5 Sept. – 22 Sept.	248	139
1996	19 Aug. – 6 Sept.	231	147

Note: DoY, middle survey day of the calendar year; IYGPT, International Young Gadoids Pelagic Trawl.

Pelagic juvenile cod were captured by a midwater trawl, IYGPT (International Young Gadoids Pelagic Trawl). This is a standard trawl designed to catch pelagic juvenile gadoids with an effective opening averaging 7.9 m high by 9.3 m wide (Anderson and Dalley 1997). The IYGPT trawl was towed at 1.25–1.5 m·s^{-1} for 30 min, slowly fishing the head rope between 20 and 50 m depth through two complete cycles. The trawl depth and configuration were monitored using acoustic net sensors (Scanmar) to measure net depth, net opening, and wing and door widths. These data were used with the distance towed to estimate the volume of water (cubic metres) filtered to standardize catch rates. The IYGPT catches were processed at sea, identifying all fish to species level where possible and recording total length and weight for dominant fish species. Sorted samples of Atlantic cod were preserved in alcohol (1994) or frozen (1995 and 1996).

Absolute abundance of pelagic juvenile cod offshore was based on the standardized catch rates at each station as

$$N_1 = \sum_{i=1}^{k} q^{-1} A C_i D_i$$

where N_1 is the absolute number of cod offshore, q is the trawl catchability, A is the area represented by each station (2.92 × 10^9 m^2), C_i is the density of cod estimated at each station (per cubic metre), D_i is the maximum tow depth (metres), and i represents the number of stations sampled offshore. For all inshore areas, absolute abundance was estimated as

$$N_2 = \sum_{j=1}^{m} q^{-1} B_j \sum_{i=1}^{k} E_i D_i$$

where N_2 is the absolute abundance inshore, q is the trawl catchability, B_j is the total area of each inshore area (square metres), E_i is the mean density of cod for all stations sampled within each inshore area (per cubic metre), D_i is the mean maximum tow depth (metres), i represents the number of stations within each inshore area, and j represents the inshore areas. The inshore areas were estimated using a high-resolution shoreline to define the inner boundary, while the outer boundary was defined arbitrarily to include an outer extension of each bay onto the adjacent shelf. Area was estimated using Surfer™ (Golden Software Inc. 1999). Total abundance for the entire stock area, 2J3KL, was simply $N_1 + N_2$. Trawl catchability was estimated for an IYGPT by Koslow et al. (1997), where $q = 0.14$. Catchability for nekton typically ranges from 0.1 to 0.25 (Sundby et al. 1989; Koslow et al. 1997).

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Table 2. Abundance, biomass, and egg production of Atlantic cod surveyed offshore in the spring of 1994–1996.

Year	Abundance	Total biomass (t)	Spawning biomass (t)	Total eggs
1994	20.2×10^6 (16.9–23.1)	17 500 (14 700 – 20 000)	11 700 (9900 – 13 400)	3.7×10^{12} (3.1×10^{12} – 4.2×10^{12})
1995	20.9×10^6 (16.4–24.9)	8 200 (6500–9800)	2 000 (1600–2400)	6.5×10^{11} (5.1×10^{11} – 7.7×10^{11})
1996	15.5×10^6 (11.5–20.0)	5 500 (4000–7000)	900 (700–1100)	2.7×10^{11} (2.0×10^{11} – 3.5×10^{11})

Note: Total eggs were estimated from abundance, maturity, and fecundity parameters for each age. Values in parentheses represent the 95% confidence intervals estimated from the acoustic survey data (see text for details).

Results

Spawning cod

The abundance of cod surveyed in Hawke Channel increased from 20 million fish in 1994 to 21 million fish in 1995 and then decreased to 16 million fish in 1996 (Table 2). Total biomass decreased from 17 500 t in 1994 to 8200 t in 1995 to 5500 t in 1996, while spawning biomass decreased from 11 700 to 2000 and finally to 900 t, respectively. The increasing abundance contrasted with a decreasing biomass resulted from the disappearance of older fish in the survey area, concomitant with an increase in demersal juvenile cod (Fig. 2). Cod age 5 and older represented 75% of all fish surveyed in 1994 and 89% of the biomass. However, in 1995 and 1996, cod age 5 and older only represented 13–14% of all fish surveyed and 31–34% of the biomass. These older cod represented the mature fish where age-5 cod were approximately 60% mature (range 38–85%) each year (Fig. 3).

During the three survey years in Hawke Channel, we measured an increase in the abundance of the 1990–1993 year-classes at ages 2–5 years (Fig. 2). This increase was probably not due to trawl selectivity, as increasing abundance occurred for cod ages and lengths considered to be fully recruited to the Campelen trawl (Godo and Walsh 1992). In addition, the 1992 year-class did not occur in the 1994 survey at age 2, but 2-year-old cod occurred abundantly in both the 1995 and 1996 surveys. In contrast, there was a significant decline in the abundance of older cod, ages 5–7 years, from the 1987–1989 year-classes. The declines in abundance of mature cod were quite severe. For example, the 1987 and 1988 year-classes disappeared entirely from the survey areas in 1995 as 7- and 8-year-old fish. In other cases, declines in abundance ranged from a decrease of 33% for cod aged 4–5 years for the 1992 year-class to 79–93% for cod aged 4–8 years for the 1988–1991 year-classes. Overall, the observations among surveys suggest a severe decline in adult cod and an in-migration of 2- to 4-year-old juvenile cod into the Hawke Channel survey area in 1995 and 1996.

The reproductive condition of cod declined significantly among years (χ^2, $P < 0.05$). In 1994, approximately 55% of the cod were mature, declining to 25% in 1995 and to 15% in 1996. In all three years, only an occasional spawning fish was encountered (<1%) and most fish were judged to be recently spent, indicating that spawning was complete by the time of the survey each year. Cod matured at very young ages in Hawke Channel, attaining >50% maturity at <5 years of age as estimated in June shortly after spawning (Fig. 3). This was similar to, but slightly younger than, the mature proportion estimated in annual autumn research vessel surveys in the 1990s (Fig. 3). We estimated that the total numbers of eggs produced each year by cod spawning in Hawke Channel declined from 3.7×10^{12} in 1994 to 6.5×10^{11} in 1995 to 2.7×10^{11} in 1996 (Table 2).

Pelagic juvenile cod

The abundance of pelagic juvenile cod decreased significantly from 3.1×10^9 individuals in 1994 to 1.5×10^9 in 1995 to 1.8×10^8 in 1996, a decrease in abundance that exceeded an order of magnitude (Fig. 4). The decline in abundance first occurred offshore in 1995, decreasing by a factor of 6 compared with 1994. Inshore, abundance remained relatively high in 1995, comparable with that of 1994. By 1996, offshore abundance declined by over two orders of magnitude compared with 1994 and over an order of magnitude compared with 1995. Inshore in 1996, abundance decreased by a factor of approximately 7.4 compared with 1994 and 1995.

Pelagic juvenile cod occurred throughout the inshore area in 1994, and they were also distributed widely offshore over the Northeast Newfoundland Shelf, although only a few cod occurred on the southern portion of the Northeast Newfoundland Shelf and on the northern Grand Bank (Fig. 5). Cod on the southern Grand Bank are managed as a separate stock (NAFO 3NO) and are not considered further here. In 1995, juvenile cod only occurred sporadically offshore over the Northeast Newfoundland Shelf, although they remained widely distributed throughout the inshore. In 1996, only a very small number of pelagic juvenile cod were found at three stations in Bonavista Bay, at one station in White Bay, and at one station off the northern peninsula. None occurred in Notre Dame Bay, Trinity Bay, or Conception Bay and juvenile cod were only observed at one station offshore.

Pelagic juvenile cod were approximately the same size each year. Cod averaged 45.1 mm (range 30–101 mm), 45.3 mm (range 27–71 mm), and 41.2 mm (range 26–62 mm) total length in 1994, 1995, and 1996, respectively. Based on microotolith analysis, these cod ranged in age from an average of 81 days in 1994 to 69 days in 1995 to 64 days in 1996 (Anderson and Dalley 2000). There was very little difference in the size and age of pelagic juvenile cod between inshore and offshore areas. For example, in 1994 when cod were distributed widely over the shelf, the length offshore was 45.0 mm compared with 44.8 mm inshore. Converting age frequency distributions to larval hatching dates demonstrated that cod spawning occurred primarily in May of 1994, whereas it occurred throughout May and June of 1995 and 1996 (Anderson and Dalley 2000). A comparison of the hatching dates between inshore and offshore areas in 1994 demonstrated that hatching started 14 days earlier inshore, but in both areas, hatching was complete by the end of June (Fig. 6). The mean hatching date was only 5 days later in the offshore.

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Fig. 2. Cod abundance estimated for each age group based on acoustic surveys in the spring of 1994 (diamonds), 1995 (squares), and 1996 (circles).

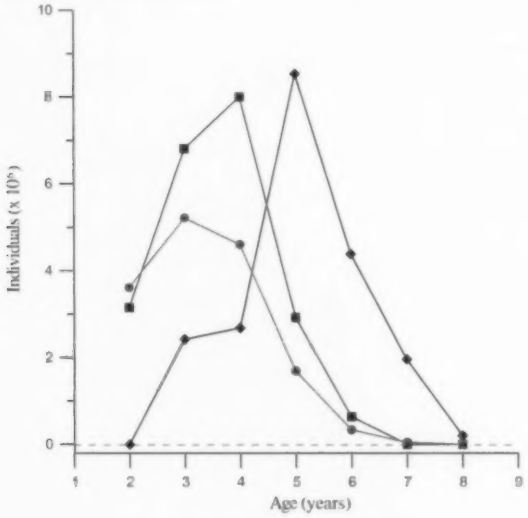
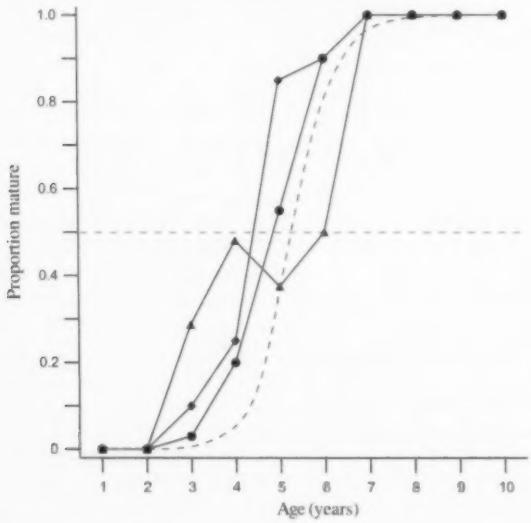


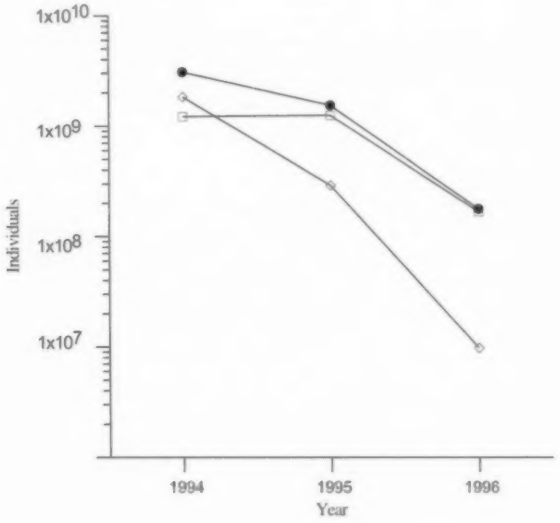
Fig. 3. Proportion of mature cod sampled in Hawke Channel during the spring of 1994 (diamonds), 1995 (triangles), and 1996 (circles) for ages 2–8 years. For reference, the average maturity at age as measured during the autumn is shown (broken line). The horizontal broken line represents 50% mature.



Mortality estimates

Declines in abundance of eggs spawned each year and the abundance of pelagic juvenile cod found offshore on the Northeast Newfoundland Shelf were in proportion, declining by over an order of magnitude among years (Fig. 7). Spawner abundance and juvenile abundance were closely associated from year to year. A simple ranking showed that the largest spawning biomass in 1994 resulted in the largest number of juveniles and the smallest biomass in 1996 resulted in the smallest number of juveniles. No further analyses were performed as a consequence of there being only 3 years of data.

Fig. 4. Abundance of pelagic juvenile cod estimated in the late summer of 1994–1996 for inshore (squares), offshore (diamonds), and total area (circles) for the cod north of 46°N latitude (NAFO 2J3KL).



We can estimate natural mortality each year from eggs to pelagic juveniles, based on our independent estimates of abundance, as

$$z = \frac{\ln(N_1) - \ln(N_0)}{t}$$

where N_0 is the abundance of eggs spawned in Hawke Channel and N_1 is the abundance of pelagic juveniles sampled offshore. Time t was the difference between mean spawning times estimated by Anderson and Dalley (2000) and the mean date of capture for pelagic juveniles. Based on this calculation, natural mortality was estimated to be –0.068·day^{-1} in 1994, –0.084·day^{-1} in 1995, and –0.112·day^{-1} in 1996. These mortalities compare with a modelled estimate of –0.081·day^{-1}, based on median parameter values for the egg–juvenile period, and a range from –0.050 to –0.111·day^{-1} for extreme parameter values (Anderson et al. 1995).

Discussion

Our data indicate that the primary cause of the poor recruitment and slow rebuilding of the northern cod in the mid-1990s has been the paucity of spawning fish, especially those spawning in the critical northern spawning grounds. It is evident that not only did the numbers of adult northern cod not stabilize or increase after the imposition of the fishing moratorium in 1992, but continued to decline. Our results suggest that this decline continued until at least 1996. Our observations support the hypothesis that repopulation of juveniles on the shelf will most likely result from northern spawning (deYoung and Rose 1993). We regard the gross re-

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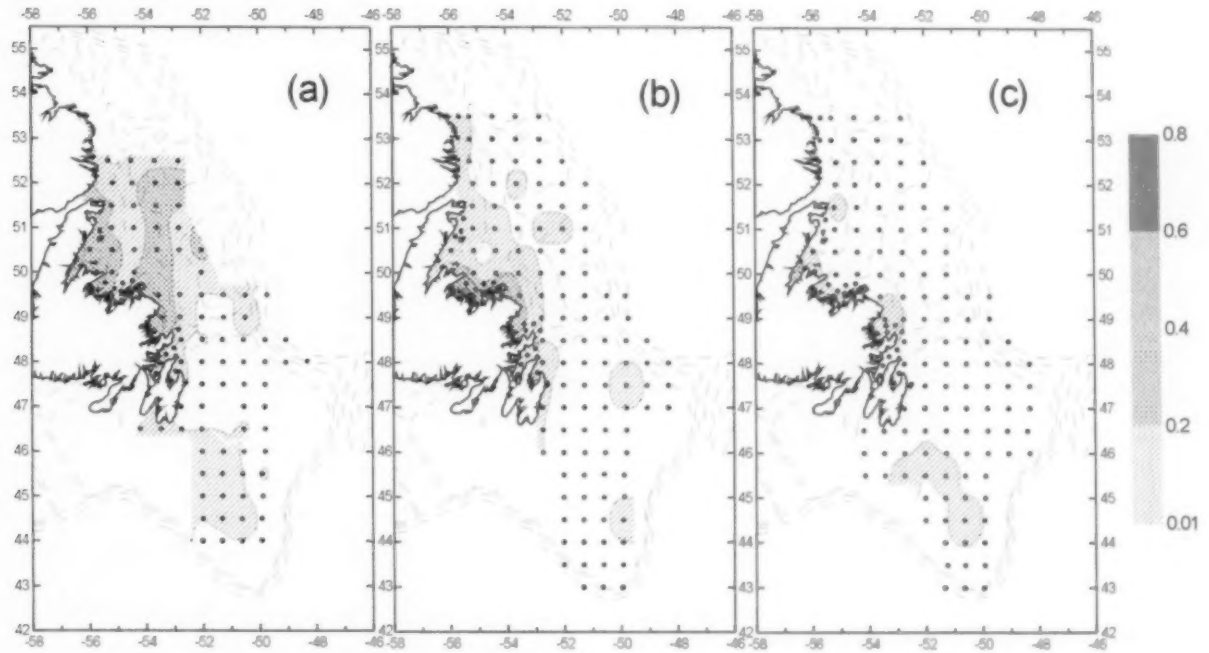
Fig. 5. Distribution of pelagic juvenile cod surveyed in (*a*) 1994, (*b*) 1995, and (*c*) 1996. The dots represent sampling stations and the blank areas are areas where no cod were caught. The contoured areas are linear intervals of $\log_{10}$-transformed abundance estimates (individuals·10^4 m^{-3}).



duction of these and other key spawning components as a form of depensation in the northern cod.

Cod in Hawke Channel were spawning at a very young age (3–5 years) compared with the historical record (see Lilly et al. 1999). Maturity data from surveys conducted in the autumn, prior to spawning the following spring, indicate an older spawning age. However, maturities estimated 6–9 months in advance of spawning are likely to include more error than those measured at or shortly after spawning (see Rideout et al. 2000). Such error may be greatest for first-time spawners.

Our data show an unexplained disappearance of adult cod from the Hawke Channel area contrasted with an in-migration of juvenile cod. In the absence of fishing, the decline in adults could have resulted either from their relocation to other spawning areas or from an increase in natural mortality. A distribution shift to the south from this same region occurred in the early 1990s (Rose et al. 2000). Could another shift have occurred in 1995? For the earlier shift, there were sufficient data to show increases in fish abundance in the southern range and evidence of northern phenotype fish in southern waters (Rose et al. 2000). Unfortunately, there are few similar data sets to test for a distributional shift in 1995. It is conceivable that these fish moved to the inshore areas along the northeast coast of Newfoundland. There is no broad-scale scientific survey designed to monitor the inshore abundance of cod that might have detected an in-migration of adults. However, local surveys have shown that there may have been a large incursion of cod into Smith Sound, Trinity Bay, in 1995. Smedbol et al. (1998) estimated that 1.83×10^{12} eggs were produced by 16 800 t (Rose 1996) of spawning cod in Smith Sound in the spring of 1995. These fish were dominated by the 1990 year-class, although there were also significant numbers of the 1986–1989 year-classes that disappeared from Hawke Channel at the same time (G.A. Rose, unpublished data). Genetic analyses on cod collected during 1992–1994 indicate that Hawke Channel fish may be genetically distinct from Trinity Bay cod and cod in the southern range (Bentzen et al. 1996; Ruzzante et al. 1996). Studies are now underway to determine the current genetic structure of Trinity Bay cod.

What might have caused such a drastic change in behavior is not known. We know that bottom water temperatures on Hamilton Bank (150 m) cooled over a decadal period from the 1980s to the mid-1990s (Colbourne 2000) and that juvenile fish are more tolerant of colder water (Goddard et al. 1992). It is possible that cooling conditions in bottom water contributed to a change in acceptable habitat for adults leading to their relocation. Capelin (*Mallotus villosus*), an important prey of cod, underwent significant changes in distribution and behavior after 1990 (Carscadden et al. 2001). Once distributed off southern Labrador in autumn, capelin no longer occurred abundantly in the north in the 1990s.

An increase in natural mortality might explain the disappearance of the adults. However, there are several factors that argue against this. Natural mortality of adults would be extremely high, on the order of 80–100%. Recently, high levels of natural mortality have been estimated for this stock, based on the offshore research trawl survey in the absence of fishing. However, these levels did not exceed 65% in the period 1993–1996 for cod aged 3–7 years (Anderson and

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Fig. 6. Larval hatching day frequencies of pelagic juvenile cod sampled from inshore (open bars) and offshore (shaded bars) areas in 1994.

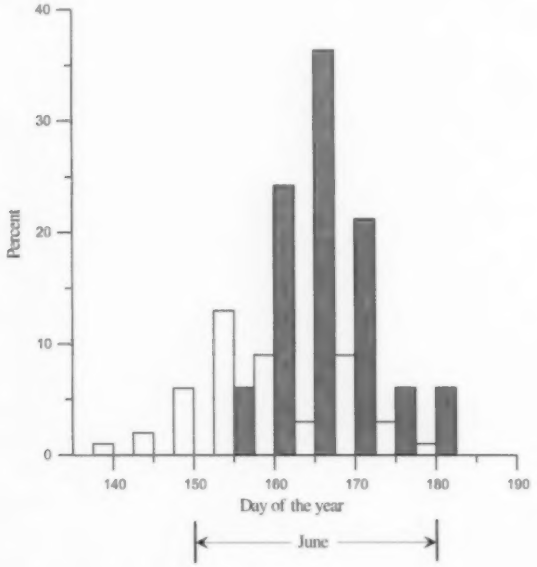
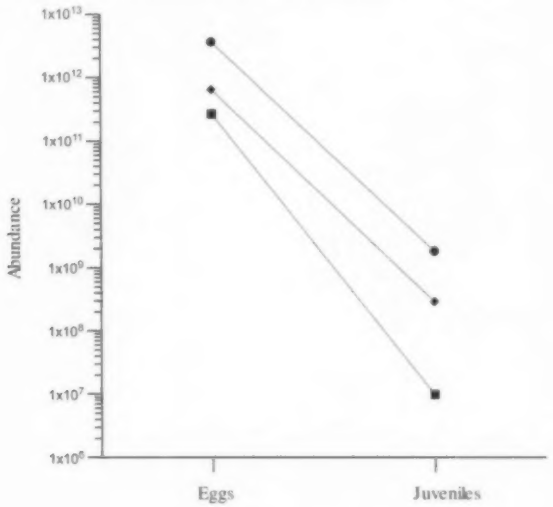


Fig. 7. Abundance of cod eggs produced each year in Hawke Channel estimated from spring acoustic surveys and the corresponding abundance of pelagic juveniles sampled offshore estimated from the pelagic fish trawl surveys. Survey years are 1994 (circles), 1995 (diamonds), and 1996 (squares).



Colbourne 2000). The research survey estimates of mortality assume that the cod remained in the offshore survey area over time, an assumption that is tenuous. Finally, any source of natural mortality would have to apply to adults only, as we measured an increase in the abundance of juvenile cod. Therefore, we find it difficult to advance the concept of an increase in natural mortality as the cause for the disappearance of adults from Hawke Channel following 1994.

Declines in fish populations at low levels of abundance and in the absence of fishing are not predicted based on historical data and the theory of compensation (Myers et al. 1997). However, the lack of recovery in the northern cod, as well as in most other cod stocks in Atlantic Canada (Swain and Castonguay 2000), has lead to the realization that depensatory mechanisms may be at work. Frank and Brickman (2000) suggested Allee effects in which the production of new fish falls to zero at low stock size. If this is the case with northern cod, the stock levels at which an Allee effect is evident must be very low indeed, as our measures of offshore spawners and juveniles declined essentially to zero in concert. Walters and Kitchell (2001) suggested a cultivation hypothesis, where predation on, or competition with, juveniles by a forage fish causes depensation. Arctic cod (*Boreogadus saida*) increased in abundance in the shelf waters off Newfoundland during the 1990s in concert with the cold-water conditions of that era (Lilly et al. 1994). Their progeny occurred simultaneously with Atlantic cod as pelagic juveniles in our juvenile fish survey. Pelagic juvenile Arctic cod are essentially the same size as Atlantic cod in late summer, presumably feeding on the same zooplankton prey. During the mid-1990s, Arctic cod juveniles outnumbered Atlantic cod by an order of magnitude or more (Dalley and Anderson 1997*b*). Hence, it is feasible that depensatory effects as hypothesized by Walters and Kitchell (2001) are evident for the period of the mid-1990s.

The lower survival rates estimated for eggs and larvae between 1994 and 1996 could be related to oceanographic factors or the biological condition of the spawners. Multispecies samples from the pelagic juvenile fish survey demonstrated that abundance decreased for many species from 1994 to 1996 and to 1997 (Anderson et al. 1999). These species included redfish (*Sebastes* sp.), Arctic cod, and American plaice (*Hippoglossoides platessoides*). All species were pelagic young-of-the-year. This common decline in 0-group abundance for different species suggests poor survival conditions during the 1994–1996 period. In addition, the remaining offshore spawners in 1995 and 1996 were from younger adults that may have been spawning for the first time. Studies elsewhere have demonstrated reduced survival from younger spawners (Trippel 1998). These factors could act in concert to effect low survival of eggs and larvae in the northern cod.

The pelagic juvenile fish survey is designed to cover the entire nursery area for cod spawned within the northern cod (2J3KL) and southern Grand Bank (3NO) stock areas, including the inshore. The close agreement between results from the spring acoustic and late-summer juvenile fish surveys suggests that the only offshore spawning during 1994–1996 occurred in the north of the 2J3KL stock area and that these spawners were greatly reduced by 1996. It is noteworthy that no concentration of adult cod was detected by the autumn offshore trawl survey in either 1993 or 1994 (Lilly et al. 1999). It appears that the traditional offshore bottom trawl survey is no longer capable of tracking population trends for the northern cod (Shelton and Healey 1999). Further, simple measures of spawning stock biomass can be an unreliable estimate of the number of viable eggs produced each year (Marshall et al.

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1998; Marteinsdottir and Thorarinsson 1998). Combining direct estimates of spawner numbers and potential fecundity in spring with the abundance of pelagic juvenile cod surviving throughout the inshore and offshore areas should provide meaningful measures of stock performance during the rebuilding phase of cod stocks.

Acknowledgements

Many people contributed to the successful completion of our surveys. E. Dalley, A. Murphy, G. Redmond, E. McDonald, D. Gillett, and D. Davis carried out the pelagic juvenile fish surveys. D. Davis was responsible for many of the data products used here. We thank the officers and crews of the *Teleost* and *Wilfred Templeman* research ships from which we conducted these surveys. G. Lilly, J. Morgan, C. Walters, and an anonymous reviewer provided insightful comments, which improved the final version of this paper. We regret the recent cancellation of the pelagic juvenile fish survey.

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Comparison of models predicting invertebrate assemblages for biomonitoring in the Fraser River catchment, British Columbia

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Abstract: A multivariate, predictive model based on the reference-condition approach is described for the Fraser River catchment in British Columbia. Benthic invertebrate assemblages and environmental descriptors were measured at more than 200 sites from 1994 to 1996, including 219 reference sites. Reference sites were classified into groups representing similar invertebrate assemblages. Five such classifications were produced, using three taxonomic levels (family, genus, and species) and species and family multimetrics. For each of the classifications, discriminant function analysis was used, with environmental descriptors, to develop a predictive model for the reference sites. These models predicted from 43.8% (species) to 61.6% (family) of the reference sites to the correct benthic group. Each model was used to assess deviation from reference condition for 21 test sites exposed to either agriculture, logging, or mining. The models were examined with regard to their sensitivity, robustness, usability, temporal variability, predictive performance, and model certainty. The family and family-metric models were ranked best, followed by the species-metric, genus, and species models. The family-level model is recommended for assessment purposes; its overall performance was slightly superior to the family-metric model and it avoids an extra step in calculation of the metrics. However, the species-level model is recommended for conservation or biodiversity issues.

Résumé : On trouvera ici un modèle prédictif multidimensionnel basé sur des conditions de référence dans l'étude du bassin versant du fleuve Fraser en Colombie-Britannique. Les peuplements d'invertébrés benthiques et les descripteurs du milieu ont été déterminés à plus de 200 sites de 1994 à 1996, y compris à 219 sites de référence. Les sites de référence ont été regroupés d'après la composition de leurs peuplements d'invertébrés. Cinq classifications ont pu être élaborées à trois niveaux taxonomiques (familles, genres et espèces) et à l'aide de métriques multiples reliées aux espèces et aux familles. Pour chaque classification, une analyse des fonctions discriminantes a permis, en utilisant les descripteurs du milieu, de produire un modèle prédictif pour les sites de référence. Ces modèles associent de 43,8% (modèle basé sur les espèces) à 61,6% (modèle basé sur les familles) des sites de référence au groupement benthique approprié. Chaque modèle a aussi servi à déterminer l'écart entre les conditions de référence et celles de 21 sites expérimentaux exposés soit à l'agriculture, soit à la coupe forestière, soit à l'activité minière. On a comparé les modèles d'après leur sensibilité, leur robustesse, leur utilisabilité, leur variation dans le temps, leur performance et leur certitude. Ce sont les modèles basés sur les familles ou les métriques reliées aux familles qui fonctionnent le mieux, suivis des modèles basés sur les métriques reliées aux espèces et de ceux basés sur les genres et les espèces. Nous recommandons donc le modèle basé sur les familles pour les études d'évaluation d'impact; son fonctionnement général est légèrement supérieur au modèle basé sur les métriques reliées aux familles et il ne requiert pas le calcul additionnel des métriques. Cependant, pour les études de conservation ou de biodiversité, c'est le modèle basé sur les espèces que nous préconisons.

[Traduit par la Rédaction]

Introduction

The Fraser River, British Columbia, is one of the last unregulated large rivers of North America. However, urban and industrial pressures pose a severe threat to the health of this ecosystem, a fact that was recognised by the establishment in 1991 of the Fraser River Action Plan (FRAP) by Environment Canada (Environment Canada 1995). A component of

Received March 22, 2000. Accepted March 20, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 12, 2001.
J15674

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 DOI: 10.1139/cjfas-58-7-1395 © 2001 NRC Canada

the FRAP was the development of a biological monitoring system for the river based on macroinvertebrate species assemblages. Thus, a programme was developed to encompass the wide range of habitat and faunal variation for this large river system.

The Fraser River biomonitoring programme is based on the reference-condition approach where the reference condition is represented by a group of minimally disturbed sites organised by selected physical, chemical, and biological characteristics (Reynoldson et al. 1997). The use of the reference-condition approach in biomonitoring requires the development of a large database of reference sites with information collected on both the assemblage of invertebrates present at each site and a matching set of habitat descriptors. From this reference database, empirical models can be constructed to predict the expected invertebrate assemblage at a site with particular habitat attributes. Such models are strictly correlative and imply no causality between the habitat variables and the biological patterns observed. In fact, some variables that are likely to have a causal relationship with the biological patterns are deliberately excluded if they are highly modified by human activity because the purpose of these models is to predict conditions in the absence of that activity.

This approach for describing the expected invertebrate assemblage at a site was first applied in freshwater systems by Wright et al. (1984). The reliable prediction of the expected assemblage at a site can be used as a baseline for assessing the status of a site that is suspected of being exposed to either chemical or physical stress. The primary objective of our study was the development of such predictive models for invertebrate assemblages that could be used as the basis of a biomonitoring program for the Fraser River catchment. Because the Fraser River catchment is extremely large (approximately 25% of British Columbia) and diverse, the approach used in developing the biomonitoring system may have applicability to other large regions or countries (Rosenberg et al. 1999).

Multivariate methods for describing and classifying assemblages with the reference-condition approach have used either presence–absence of taxa, as in the United Kingdom (Wright et al. 1984) and Australia (Parsons and Norris 1996), or abundance of taxa, as in Canada (Reynoldson et al. 1995, 1997). A second approach to using reference conditions is based on additive indices from a subset of derived measures called metrics (e.g., number of taxa, percentage of total individuals that are Ephemeroptera) and is used widely in the United States (Karr 1991; Barbour et al. 1995, 1996). Therefore, another objective of our study was a comparison of multimetric variables with taxonomic counts using multivariate methods.

There has been considerable debate in the biological monitoring literature on the necessary level of taxonomic resolution required to detect environmental impairment. This question is not easily resolvable and partly depends on the question being asked (Resh and McElravy 1993). There are essentially two positions: (*i*) because organisms have evolved species-level tolerances to various stressors, identification at this level is most appropriate to detect response to impairment, and (*ii*) higher levels of taxonomic resolution are adequate for detecting assemblage response, and the savings in both time and resources justify the loss of some information. Our final objective was to determine the appropriate taxonomic level for the Fraser River biomonitoring programme.

Rosenberg et al. (1999) outlined why the reference-condition approach was chosen as the basis of the Fraser River biomonitoring programme, the criteria for choosing reference sites, the variables to be measured at each site, and the development of the sampling protocol. This paper describes (*i*) the results of sampling invertebrate assemblages and habitats from more than 200 reference sites, (*ii*) the development of predictive models using the reference condition from the reference site database at different taxonomic levels and with data derived from invertebrate metrics, and (*iii*) the effectiveness of lower-taxon (genus and species) versus family-level identifications in establishing reference site groups and identifying possibly impaired sites.

Methods

Study area and sampling sites

The Fraser River catchment covers approximately 230 000 km^2 of British Columbia, Canada's westernmost province (B.C. Ministry of Environment, Lands and Parks and Environment Canada 1993). The Fraser River itself has a mean annual discharge of 3620 $m^3 \cdot s^{-1}$, which makes it the sixth largest river in North America (Dynesius and Nilsson 1994), with approximately 1 700 000 people living in the catchment.

The multivariate methods used in the reference-condition approach require sufficient sites to characterise variability in the catchment associated with reference conditions. No absolute guideline exists for the total number of sites required, although other studies (e.g., Reynoldson et al. 1995; Wright 1995; Reynoldson and Wright 2000) suggest that approximately 250 are required to characterise variability adequately and to build appropriate predictive models.

Two stratification levels were used to encompass the range of conditions within the study area. First, the ecoregion level ensured that the range of climatic and landscape conditions were included in the reference sites selected. The ecoregions used were based on previous studies by Demarchi (1990) and the B.C. Ministry of Environment, Lands and Parks (1991). Second, stream order (Strahler 1964) ensured that a wide range of hydraulic conditions were included in the reference sites selected.

There were two steps in site selection. First, a series of workshops with provincial experts served to identify non-, moderately, and heavily impacted subcatchments and to choose subcatchments that were distributed through as many ecoregions as possible. Reference subcatchments slated for sampling were then outlined on 1 : 250 000 maps and stream orders were identified using the Strahler (1964) method. Two or three sites were randomly located on each stream order within a subcatchment. A "site" was considered to be a stream reach with a longitudinal distance approximately six times its width (Newbury 1984). Only erosional (i.e., riffle–run) reaches were sampled because they were the dominant habitat type; sampling of other habitat types would have taken more time, and multiple-habitat sampling often provides redundant data (Parsons and Norris 1996). The second step was field verification, which involved either land-based or aerial (via helicopter) surveys of the area surrounding the site to confirm that it was not impacted. Occasionally, site locations were moved during the field operation because the original ones were inaccessible or because the identified streams were dry; however, the distribution of sites among stream orders was maintained.

A total of 219 reference sites were sampled over the 3-year study period, together with 21 test sites related to specific human

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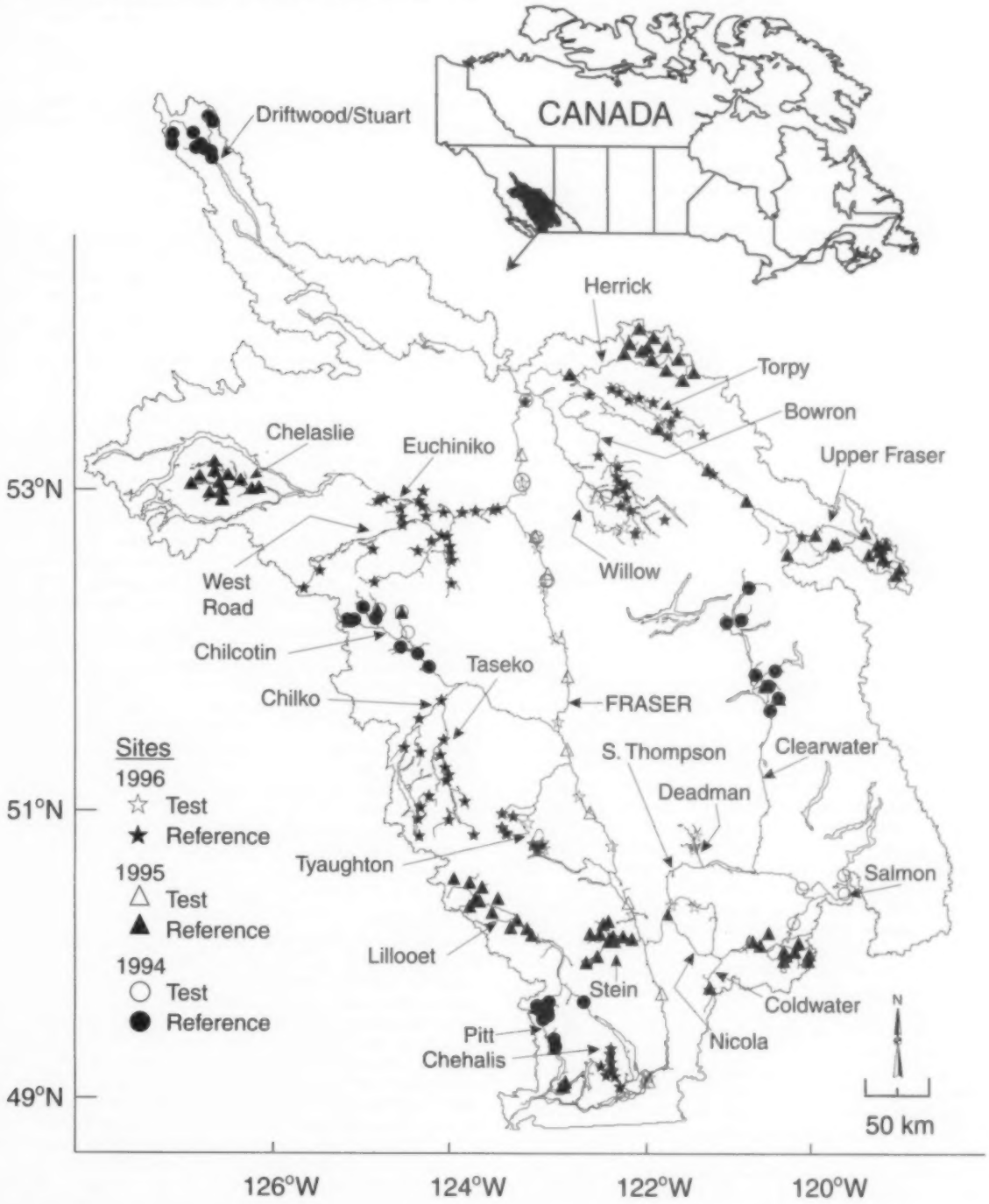
Fig. 1. Location of test and reference sites sampled during 1994–1996 in the Fraser River catchment.



activities (agriculture, logging, and mining) (Fig. 1). The large number of reference sites required a sampling program that was staged over 3 years: approximately 50 sites were sampled in 1994 and approximately 100 sites in each of 1995 and 1996. Most of the reference sites were visited only once, in autumn, because of the large geographic scale of the study. The autumn period was chosen because it represented a low-water period in the long-term hydrograph of the Fraser River, which was important in terms of accessibility to streams in the catchment. Because predictive models developed from this reference database could, therefore, be constrained to an annual autumn sampling, we examined the effects of seasonal variability on the accuracy of the predictive

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models. Seasonal variation was examined by seasonal sampling of a subset of sites (Reece et al. 2001). We examined annual variation by revisiting 14 sites in either or both years 2 and 3 of the study (Rosenberg et al. 1999).

Reference sites were distributed over 11 ecoregions (Rosenberg et al. 1999). The number of sites per ecoregion ranged from three in the Lower Mainland to 56 in the Fraser Plateau. Sites were located in 21 different subcatchments. Seven stream orders were sampled and the median stream order was 3 (Table 1). Sites ranged in altitude from 30 m above sea level (to a maximum of 2000 m above sea level, stream width ranged between 0.4 and 226.8 m (median 9.8 m), and sampling depth ranged between 5 and 73.3 cm (median 24.2 cm). The ranges for other variables are summarised in Table 1.

Sampling methods

Benthic invertebrates were collected at each site with a single travelling kicknet sample (400-µm mesh) of 3-min duration (Rosenberg et al. 1999). A triangular kicknet (38.5 cm to the side) was chosen over other possibilities because it was inexpensive to construct and easy to transport and use. A calibration study on the Coldwater River, a tributary to the Nicola River (Fig. 1), examined optimal operating characteristics of the kicknet: (*i*) number (1–10) of replicates, (*ii*) sampling time (1, 3, or 5 min), (*iii*) differences among three operators, and (*iv*) differences between two mesh sizes (200 and 400 µm). Based on the results from this study (Rosenberg et al. 1999), five replicates per site were selected. However, subsequent analysis of 22 reference sites showed high within-site precision, and for the remaining sites, only one kicknet sample per site was taken. No significant differences (analysis of variance (ANOVA), $p > 0.05$) existed among the three operators in terms of total numbers or numbers in the four major orders collected. The apparent robustness of the kicknet sampling method was reassuring because there was no difference between an inexperienced operator and two experienced operators. No significant differences (ANOVA, $p > 0.05$) existed among the three time intervals for total numbers or numbers in the major orders, which were all corrected to reflect number per minute. However, the number of taxa collected in 1-min samples was significantly ($p < 0.05$) lower than in the 3- and 5-min samples. Therefore, 3 min was adopted as the standard collection time. The 200-µm-mesh nets retained significantly higher numbers than the 400-µm-mesh nets (ANOVA, $p < 0.05$). However, the overall number of taxa collected was similar in both mesh sizes ($p > 0.05$). Consequently, we decided to use 400-µm mesh for the remainder of the study for purely practical reasons: the 200-µm-mesh samples took approximately 8 days·replicate^{-1} to process, which precluded the use of this mesh size in a large-scale study.

Entire samples were subsampled using a 100-cell Marchant box (Marchant 1989). Organisms were identified to the lowest possible taxon. The appropriate subsample size was examined at four sites (Rosenberg et al. 1999), and based on this analysis, a 200-organism subsample was counted from each sample. The number of cells counted for a 200-organism subsample was recorded, and the count for a site was adjusted back to a whole-sample estimate to provide the relative abundance at each site. Data were recorded as the number of organisms per 3-min kicknet sample.

Forty environmental variables were measured at each site (Table 2). These variables were selected based on their relevance to site characterisation (Rosenberg et al. 1999) and represented four different categories of variables (landscape, site/reach, channel/substrate, and water column). A detailed description of the sampling methods used is available in Rosenberg et al. (1999).

Taxonomic resolution

To examine the implications of taxonomic resolution, data were analysed and predictive models were developed for five data sets: "species" (lowest practical level, in some cases the generic level; morphospecies were not designated because of the effort involved in a study with so many sampling sites), genus, and family levels in taxonomic composition and abundance models and family and "species" for metric models. We refer to these five data sets throughout the manuscript as the family-assemblage model, genus-assemblage model, species-assemblage model, family-metric model, and species-metric model.

Assemblage metrics

The biological monitoring approach that is widely used in the United States involves metrics, which incorporate ecological knowledge about the responses of invertebrate assemblages present at a site (Resh and Jackson 1993). We initially examined 59 metrics, 28 using family-level information and 31 using the species level. Because metrics have a built-in redundancy (e.g., No. EPT (Ephemeroptera, Plecoptera, and Trichoptera) taxa and No. Ephemeroptera taxa), we reduced the number of metrics by examining the relationships between them using ordination and correlation analysis at both species and family taxonomic levels. We selected metrics by conducting a preliminary ordination and ranking of the metrics from their correlation with the overall ordination structure, as indicated by the correlation coefficient for each metric derived from principle axis correlation (see below), and also by conducting a correlation analysis between the highest ranked metric and all other metrics. A metric was retained if the probability of correlation was low ($p > 0.0001$). This procedure was repeated with the next highest ranked metric until a final list was established.

The metrics used in the creation of the reference database are summarised in Table 3. At the species level, the metric total taxa contributed most to the ordination and thus had the greatest amount of information; it had the highest correlation with the ordination axes ($r = 0.8471$) (Table 3). However, the next eight highest ranked metrics (Table 3) were very significantly correlated ($p < 0.0001$) with total taxa and thus were eliminated from subsequent analyses. The next highest ranked metric to be included in subsequent analyses was % Chironomidae. The same correlation analysis was done for it and subsequent metrics to produce a final list of nine species-level metrics (Table 3). The same approach produced eight nonredundant family-level metrics: % EPT individuals, total taxa, total individuals, % Coleoptera, % Trichoptera as Hydropsychidae, % Diptera as noninsects, % Ephemeroptera as Baetidae, and % gatherers.

Data analysis

Multivariate methods were used for classifying reference sites, matching test sites with appropriate reference site groups, and comparing test sites and reference sites to determine impairment. These methods were used to describe and classify the invertebrate assemblages, to develop the predictive models based on the relationships between the invertebrate and habitat data sets, and to compare the test sites with appropriate reference sites. Reynoldson et al. (1997, their fig. 1) described the four steps in using reference sites to characterise the biological conditions of a region and how to compare test sites with an appropriate subset of reference sites: (*i*) the collection of data on invertebrate assemblages and habitat characteristics at a range of reference sites, (*ii*) the classification of sites into groups using clustering methods based on the similarity of their taxonomic composition, (*iii*) the development of a predictive model based on the reference site groups using discriminant function analysis with selected habitat characteristics, and (*iv*) the comparison of a test site with one of the reference-site groups, selected by application of the predictive model. Test site(s) and reference sites are compared in taxonomic ordination space. These steps involve fairly complex analysis, which is described in some detail below.

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Table 1. Range of selected site descriptors for 219 reference sites sampled in the Fraser River catchment.

Variable	Minimum	Maximum	Median
Stream order	1	7	3
Altitude (m above sea level)	30	2000	970
Channel width (m)	0.4	226.8	9.8
Mean depth (cm)	5	73.3	24.2
Mean velocity ($m \cdot s^{-1}$)	0.075	1.254	0.406
Alkalinity ($mg \cdot L^{-1}$)	0	201	38.1
Total suspended solids ($mg \cdot L^{-1}$)	0.4	168.0	7.1
Total phosphorus ($mg \cdot L^{-1}$)	0.000	0.149	0.008
Nitrate/nitrite ($mg \cdot L^{-1}$)	0.001	0.334	0.013
pH	5.6	9.3	7.7
Conductivity ($\mu S \cdot cm^{-1}$)	4.6	426.0	92.0
Dissolved oxygen ($mg \cdot L^{-1}$)	5.0	14.8	11.8
Framework (category, Table 2)	1.0	8.0	6.0
Matrix (category, Table 2)	0.0	8.0	3.0
Embeddedness (category, Table 2)	1.0	5.0	4.0

Classification of reference sites

Classification methods were used to describe the structure of the biological data used for the three assemblage and two metric models. It is well known that distributional patterns revealed by multivariate analysis of benthic invertebrate assemblages are the result of the contributions made by common taxa; rare taxa have low information content and tend mainly to add noise to the data set (Norris et al. 1982; Marchant 1990). At the family level, 74 taxa were identified and used. At the genus level, 223 taxa were identified. At the "species" level, 318 taxa were considered: 123 species, 31 species groups, and 164 genera. In the case of the genus-assemblage and species-assemblage models, most of the taxa were rare; only 26 of 223 genera and 25 of 318 "species" represented ≥1% of the total organisms collected. Therefore, we eliminated from the data analyses all taxa that occurred at <5% of the sites (Field et al. 1982; Clarke and Warwick 1994). This procedure resulted in 124 "species" and 97 genera being used in the classification.

For the three assemblage models, the counts for each taxon from a 3-min kicknet sample were used as descriptors of the benthic invertebrate assemblage. The data were not transformed because we wanted to weight numerically dominant taxa. The Bray–Curtis association measure was used as an association metric for the benthic invertebrate counts because it performs consistently well in a variety of tests and simulations using different types of data (Faith et al. 1987; Jackson 1993). The Canberra (Jaccard) metric was used as an association measure for the two metric models, as recommended by Legendre and Legendre (1998, their tables 7.3–7.5).

The reference sites were clustered using agglomerative hierarchical fusion, the unweighted pair-groups method with arithmetic averages (UPGMA). The appropriate number of groups was selected by examining the group structure and, particularly, the spatial location of the groups in ordination space. A minimum group size of 10 sites was selected and used as the stopping rule for the classification (Wright 1995). Groups formed with fewer than 10 sites were considered to be too small to sufficiently describe normal variability and to be useful for comparison with test sites.

Ordination was also used to describe and explain the variability observed among the large number of taxa with a reduced number of new variables (ordination axes). In this analysis, we used a hybrid multidimensional scaling (HMDS) method of ordination that incorporates both metric and nonmetric scaling (Faith et al. 1987) and that is of particular value when relating ordination scores to environmental characteristics. All clustering and ordination was done using PATN, a pattern analysis software package developed by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) in Australia (Belbin 1993).

Prediction of site groups

An important feature of the reference-condition approach is the selection of an appropriate subset of the total number of reference sites that is used in assessing any new test site. The subsets of reference sites were established by the grouping of similar sites using cluster analysis, as described above. Discriminant function analysis (DFA) was used for predicting the reference group to which a test site was expected to belong. In this method, descriptions of the habitat are used to classify sites into the groups formed by the invertebrate data.

Twenty-nine of the 40 environmental variables measured in this study (Table 2) were considered for use in predictive models of the biological structure of the data. Variables were excluded from initial consideration as predictors for either of two reasons. First, they were excluded if they were likely to be influenced by anthropogenic activity (e.g., nutrient enrichment, physical disturbance), which is important because the predictive models are used to establish what community would occur at a test site unaffected by human activity. Second, variables were excluded if temporal variability would result in a single measurement being unrepresentative (e.g., temperature, dissolved oxygen).

Selection of appropriate variables for use in predictive models was done in two ways. The first one used principal axis correlation (PAC, procedure PCC in PATN), which determines how well a set of attributes (environmental data) can be fitted to a second set of variables (biota) in ordination space. This method is a multiple-linear regression that takes each environmental attribute and determines the location of the vector that has the best fit in ordination space. The variables can be represented as an axis on an ordination plot, and a correlation of the variable with the ordination is provided. A randomisation model was used to establish the statistical significance of the correlation. The second way used stepwise DFA (procedure STEPDISC in SAS; SAS Institute Inc. 1988) to establish which environmental variables best separated sites into the predefined groups formed by classification of the biological data set. Stepwise selection of variables was used, and the significance level for variable entry and retention was 0.05.

The concern of Legendre and Legendre (1998) that relationships between biological response and habitat attributes may not be optimal if they do not consider spatial organisation was addressed by examining the spatial component of variation in potential habitat

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Table 2. Environmental variables measured in the Fraser River biomonitoring programme.

Environmental variable	Abbreviation	Unit of measurement or no. of categories
Landscape		
Latitude[a,b]	LAT	Decimal degrees
Longitude[a,b]	LON	Decimal degrees
Altitude[a,b]	ALT	Feet above sea level
Ecoregion[a]	ECOR	11 categories
Stream order[a]	SORD	7 categories
Site/reach		
Date of sampling		1–365
Flow state[c]	FLOW	3 categories
Macrophyte cover[d]	MCPHYT	5 categories
Grasses[e]	GRASS	2 categories
Shrubs[e]	SHRUB	2 categories
Conifers[e]	CONIF	2 categories
Deciduous[e]	DECID	2 categories
Riparian vegetation[f]	RIPAR	1–10
Canopy cover[g]%		
Extent of logging in riparian zone[d]		5 categories
Channel/substrate		
Wetted width	WIDTH	m
Mean depth[h]	MNDEP	cm
Maximum depth[h]	MXDEP	cm
Bankfull width	BNKWI	m
Slope	SLOPE	$m \cdot m^{-1}$
Mean water velocity[i]	MNVEL	$m \cdot s^{-1}$
Maximum water velocity[i]	MXVEL	$m \cdot s^{-1}$
Framework[j]	FWORK	7 categories
Matrix[k]	MTRX	7 categories
Embeddedness[l]	EMBED	5 categories
Interstitial material		
Gravel[m]	GRVL	%
Sand[m]	SAND	%
Silt[m]	SILT	%
Clay[m]	CLAY	%
Benthic algae biomass[n]		$mg \cdot L^{-1}$
Benthic algae chlorophyll *a*[n]		$mg \cdot L^{-1}$
Water column		
pH	PH	
Dissolved oxygen	DO	$mg \cdot L^{-1}$
Alkalinity	ALK	$mg \cdot L^{-1}$
Conductivity	COND	$\mu S \cdot cm^{-1}$
Temperature		°C
Total phosphorus	TP	$mg \cdot L^{-1}$
Nitrate/nitrite	NO3	$mg \cdot L^{-1}$
Total Kjeldahl nitrogen	TKN	$mg \cdot L^{-1}$
Total suspended solids	TSS	$mg \cdot L^{-1}$

Note: The 29 variables used in data analyses are identified (bold) together with their abbreviations and some information on data collection.
[a]Obtained from 1 : 250 000 topographic maps.
[b]Using onboard GPS.
[c]Recorded as follows: 1, riffle/rapids; 2, straight run; 3, pool/back eddy.
[d]Recorded as follows: 1, 0%; 2, 0–25%; 3, 25–50%; 4, 50–75%; 5, 75–100%.
[e]Recorded as present (1) or absent (0).
[f]Summed score of four vegetation categories present: 1, grass; 2, shrubs; 3, conifers; 4, deciduous.
[g]Based on visual observation of the site.
[h]Based on sampling area; represents the complete channel in wadeable streams.
[i]Based on a minimum of five estimates with a flowmeter.
[j]Dominant particle size in sampling area: 1, <0.2 cm; 2, 0.2–0.5 cm; 3, 0.5–2.5 cm; 4, 2.5–5 cm; 5, 5–10 cm; 6, 10–25 cm; 7, >25 cm.
[k]Material surrounding dominant particles: 1, <0.2 cm; 2, 0.2–0.5 cm; 3, 0.5–2.5 cm; 4, 2.5–5 cm; 5, 5–10 cm; 6, 10–25 cm; 7, >25 cm.
[l]Estimated in sampling area: 1, completely embedded; 2, 75% embedded; 3, 50% embedded; 4, 25% embedded; 5, unembedded.
[m]From sedigraph particle size analysis (Duncan and LaHaie 1979) of the interstitial material.
[n]Based on a mean value of a 4-cm-diameter sample taken from three separate rock surfaces (Rosenberg et al. 1999).

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Table 3. Species-level metrics and correlation of individual metrics with the ordination matrix (ranked by contribution to the ordination structure).

Species-level metric	Correlation with ordination structure	Correlation of metric with total taxa	Probability level of correlation of metric with total taxa
Total taxa	0.8471	1.000	0.0000
% Chironomidae	0.7393	0.246	0.0071
Total individuals	0.6012	0.306	0.0001
Plecoptera	0.4811	0.222	0.0269
% gatherers	0.4435	–0.123	1.0000
% Trichoptera as Hydropsychidae	0.3337	0.111	1.0000
% Ephemeroptera as Baetidae	0.2386	0.076	1.0000
% predators	0.1961	0.124	1.0000
% Diptera as noninsects	0.1381	–0.058	1.0000

Note: The correlation (and probability) of each metric with the total taxa metric is also shown. Metrics not significantly correlated ($p > 0.0001$) with a higher-ranked metric were used in subsequent analysis. EPT is Ephemeroptera, Plecoptera, and Trichoptera. Other metrics considered but discarded because of correlation ($p < 0.0001$) with another metric were % EPT individuals, biotic index, % five dominant taxa, Diptera, Trichoptera, Chironomidae, EPT taxa, % two dominant taxa, % dominant taxa, EPT/Chironomidae + EPT, % scrapers, Coleoptera, % Plecoptera, % Plecoptera, % Tanytarsini, % filterers, % gatherer-filterers, Ephemeroptera, number of predators, % Trichoptera, % Coleoptera, % Ephemeroptera, and % shredders.

predictors. Correlation analyses between latitude and longitude and each of the 27 other potential predictor variables (Table 2) showed that only three of 14 continuous variables had significant relationships (Pearson correlation analysis, $p < 0.05$), with latitude only, and in all cases, the r^2 values were low (altitude: $r^2 = 0.04$; conductivity: $r^2 = 0.05$; alkalinity: $r^2 = 0.09$). Of the 13 categorical variables examined (Spearman correlation analysis; significance test not available), only three had r^2 values >0.10 (longitude and the presence of grasses: $r^2 = 0.11$; latitude and substrate framework: $r^2 = 0.12$; longitude and ecoregion: $r^2 = 0.29$). A relatively strong spatial correlation with ecoregion could be expected. Therefore, we concluded that, overall, spatial structure of the data was not a major source of false correlation in our data.

Based on PAC and stepwise DFA, environmental variables were used in DFA to establish functions for the variables that best separated sites into the predefined biological groups. The SAS version of DFA (procedure DISCRIM in SAS; SAS Institute Inc. 1988) was used with raw environmental data to generate discriminant scores and to predict the probability of group membership. The accuracy of predictions from the discriminant model was verified by examining how well the reference sites were predicted to the correct group. The predicted groupings and actual groupings were then compared to provide a group and total error rate.

Final selection of the optimal predictor variables was done by iteration. Various combinations of predictor variables were selected based on the results of the stepwise DFA and PAC. The optimal set was defined as that with the lowest error rate from cross-validation in DFA (Moss et al. 1987; Parsons and Norris 1996).

Assessing test sites

The reference-condition approach assumes that a set of reference sites describes normal or unimpaired conditions and that the quality of a test site is determined by the degree of similarity between the test site and the reference sites. To assess a test site, it is first predicted to one of the reference site groups formed from the original classification, using the predictive model constructed from DFA. Variation among the reference sites, in the group to which the test site is predicted, is assumed to represent the normal range of variation expected at the test site if it is unimpaired. To determine the similarity between the test site and the appropriate reference sites, both the reference sites and the test sites are ordinated and plotted in ordination space. If the test site falls within the "cloud" of sites representing the reference condition, then it is considered to be equivalent to reference; if it is outside the reference site cloud, it is considered to be different from reference. Construction of Gaussian bivariate probability ellipses (Altman 1978; Owen and Chmielewski 1985) in SYSTAT (procedure Scatterplot) around the reference sites defines the bounds of the reference site cloud. The degree of difference or similarity between the test site and the reference site cloud can be quantified by using different probability ellipses (see the example below in the Results section). The greater the departure from the reference state, as measured in ordination space, the greater the difference from the reference condition.

Wright et al. (1991) developed a method that used a series of bands, representing grades of biological quality from good to poor, to provide a simple statement of biological quality, which allowed broad comparisons in either space or time that would be useful for management purposes. For the Fraser River catchment, we established four categories or bands of biological quality based on how similar a test site is to the reference sites, using probability ellipses. Band 1 is inside the smallest ellipse (90% probability) around the reference sites and is "equivalent to reference," Band 2 is between the smallest (90%) and next ellipse (99% probability) and is "possibly different from reference." Band 3 is between the 99% probability and the largest ellipse (99.9% probability) and is "different from reference," and Band 4 is outside the 99.9% ellipse and is "very different from reference." If three ordination axes were required to describe the variation in the invertebrate assemblage, then sites were plotted on all three axes and the greatest difference from reference was used to assign the status of a test site.

The discriminant model was run for each of 21 test sites exposed to human activity, and each test site was compared with the group of reference sites to which it was assigned the highest probability of belonging and to any other group to which it had >25% probability of belonging. A test site was assessed as being equivalent to reference, possibly different, different, or very different by being plotted in ordination space with the reference sites to which it had the greatest probability of belonging, as described above.

Comparison of models

The advantages and disadvantages of the five models were assessed using seven measures: (*i*) sensitivity, (*ii*) robustness, (*iii*) usability, (*iv*) annual variability, (*v*) seasonal variability, (*vi*) predictive performance, and (*vii*) model certainty.

The sensitivity ranking was determined by simply summing the number of assessments to each band, scoring a Band 1 as 1, Band 2 as 2, etc.; the most sensitive model was the one with the highest overall score. The robustness of the models was determined by the consistency of assessments. There were two aspects to the usability

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Table 4. Species richness (average number of species (±SD) per 3-min kicknet sample), species abundance (average number of individuals (±SD) per 3-min kicknet sample), and taxa considered as very common among eight groups of reference sites formed by cluster analysis of 123 species for the Fraser River catchment.

Group	Species richness	Total abundance	Very common species (present at ≥70% of sites) in a group
1	22.9 (5.0)	1 917 (1437)	*Rhithrogena* spp. (95%) *Capnia* spp. (81%) *Taenionema* spp. (81%) *Drunella doddsi* (78%)
2	21.4 (7.6)	302 (141)	*Rhithrogena* spp. (95%) *Drunella doddsi* (90%) *Taenionema* spp. (90%) *Baetis bicaudatus* (85%) *Capnia* spp. (80%)
3	13.6 (4.7)	1 462 (1349)	*Taenionema* spp. (100%) *Rhithrogena* spp. (94%) *Drunella doddsi* (78%)
4	15.7 (6.1)	290 (306)	*Ameletus* spp. (72%)
5	24.5 (4.9)	1 263 (1239)	*Rhithrogena* spp. (86%) *Sweltsa* sp. (86%) *Paratrichocladius* sp. (79%) *Ephemerella* spp. (71%)
6	22.6 (5.7)	7 263 (4781)	*Baetis bicaudatus* (100%) *Micropsectra* spp. (100%) *Taenionema* spp. (75%) *Capnia* spp. (70%) *Rhithrogena* spp. (70%)
7	24.1 (6.2)	12 207 (7658)	*Micropsectra* spp. (92%) *Capnia* spp. (75%) *Tvetania bavarica* (75%)
8	26.5 (5.2)	7 553 (6145)	*Micropsectra* spp. (82%) *Sweltsa* spp. (74%) *Polypedilum* spp. (72%)

of the models: the laboratory requirements and steps involved in preparing data for analysis (e.g., sample processing, sorting, identification) and the steps involved in data processing and analysis. The importance of annual variation on the ability to predict invertebrate assemblages was assessed by examining the stability of the assemblage at a site from year to year (Rosenberg et al. 1999). A site was considered to have a stable assemblage if it appeared in the same faunal group in each sampling year. The effect of seasonal variability on the performance of the models was examined by Reece et al. (2001), who compared the performance of genus- and family-assemblage models for six reference sites sampled seasonally. The predictive performance was assessed from the results of the cross-validation of the reference sites in the DFA. Last, model certainty was determined from the average of the probabilities of group membership from the 21 test sites for each of the models. The higher the probability that a test site belongs to a group, the greater is the certainty of the prediction. In summarising the overall performance of the five models, we simply rank-ordered them based on the seven attributes because several of these attributes were categorical.

Results

Classification of sites

Cluster analysis of the three taxonomic and two metrics data sets produced from four to eight groups, using a 10-site minimum group size (data not shown). There were differences among the five classifications. Less structure was evident in the metrics data than in the taxonomic data, as indicated by lower ultrametric scores, the smaller number of groups formed, and the number of groups containing only a few sites. In fact, the species-metric dendrogram first split into a group of one site, and only three additional groups were evident. In the taxonomic classifications, the amount of structure in the data (i.e., the number of groups formed) increased from family (four groups) to species level (eight groups).

The classification at the species level illustrated the biological diversity of invertebrate assemblages in the Fraser River catchment (Table 4). The cluster analysis first separated Groups 6, 7, and 8 from Groups 1–5. Groups 6 and 7 had high abundance and high species richness. Groups 2 and 4 had the lowest abundance, and Groups 3 and 4 had the lowest species richness. The most frequently occurring taxa (very common taxa, present at >70% sites) in each group are listed in Table 4. The least productive and taxonomically rich sites (Groups 2 and 4) were the high-order, large rivers (based on bankfull and wetted stream width), which were associated with the absence of grass in the riparian zone (Table 5). Groups 2 and 4 also had low total phosphorus (Table 5). The groups with the greatest abundance and species richness (Groups 6–8) had high alkalinity, high Kjeldahl nitrogen, and a high proportion of grass in the riparian zone and were either small streams (Groups 6 and 7) or had high total phosphorus (Groups 6 and 8) (Table 5).

Three spatial scales existed at which assemblage structure could be described and compared: (*i*) the entire Fraser River catchment, where little pattern was visually evident (Fig. 2), (*ii*) the subcatchment, where broad patterns appeared, and (*iii*) the site, where there was a tendency for one site to belong to the same group as a nearby site (Fig. 2). Across the entire Fraser River catchment, faunal Groups 1 and 7 included sites from 14 and 15 of the 21 subcatchments, respectively. Sites in these groups occurred from the Stuart River in the north to the Pitt River in the south and the Chelaslie River in the west to the Upper Fraser River in the east. Group 3 was most geographically restricted; all but two sites were in two southern rivers, the Pitt and Lillooet. A strong spatial signal was associated with subcatchments. For example, Group 8 primarily represented sites in the west-central part of the catchment, the Chilcotin, Chelaslie, and West Road rivers in the Fraser Plateau ecoregion (Fig. 2). Group 4 represented Upper Fraser and Fraser River sites, and Group 3 represented all but one site from the southern coastal range, primarily the Pitt and Lillooet rivers (Fig. 2). The smallest-scale patterns, in which sites within a river system tended to be in the same group, included the Herrick, where sites on the main river were in the same group (Group 1) but sites on the smaller tributaries belonged to other groups (Fig. 2). Similarly, in the Lillooet River, upstream sites belonged to Group 3 and downstream sites were in Group 2. Headwater sites represented by faunal Group 6 were located across the Fraser River catchment (nine subcatchments).

Predicting group membership

The relationships from PAC between the 29 variables con-

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Table 5. Habitat characteristics (means) that were very significantly different ($p < 0.0001$) among eight groups of Fraser River reference sites from cluster analysis of 123 species.

Group	Stream order	Latitude (decimal degrees)	Altitude (m above sea level)	Grasses (% sites with grass present)	Bankfull width (m)	Width (m)	Average velocity ($m \cdot s^{-1}$)	Alkalinity ($mg \cdot L^{-1}$)	Framework (see Table 2)	TP ($\mu g \cdot L^{-1}$)	TKN ($\mu g \cdot L^{-1}$)
1	2.4	52.41	3602	35	40	19	0.45	36.1	6.3	7.3	61
2	3.0	50.92	2252	10	70	28	0.61	32.5	6.8	13.7	36
3	2.4	50.56	2467	13	90	17	0.52	17.6	7.4	16.9	29
4	3.7	52.92	3136	11	108	67	0.38	45.3	5.8	9.9	70
5	3.0	50.62	2463	7	49	23	0.45	21.8	6.7	9.8	52
6	2.0	53.00	3720	40	13	7	0.36	51.4	5.8	20.4	180
7	2.1	52.49	3960	68	28	12	0.34	50.6	4.9	13.9	184
8	3.8	52.51	2963	56	37	19	0.48	57.2	5.9	41.5	201

Note: TP, phosphorus; TKN, total Kjeldahl nitrogen.

sidered to be suitable predictors (Table 2) and the ordination matrices from the five data sets were examined individually (data not shown). The presence of grasses in the riparian zone showed the strongest correlation in all five analyses (r = 0.447–0.539). Other environmental variables were strongly correlated with the ordination axes of the invertebrate assemblages and metrics: stream width and bankfull width (both median rank 3, r = 0.298–0.447), framework (rank 4, r = 0.345–0.432), alkalinity (rank 5, r = 0.339–0.464), mean velocity (rank 6, r = 0.227–0.391), and average depth (rank 7, r = 0.281–0.336). Variables that showed the weakest relationship with the invertebrate assemblages and metrics were occurrence of conifers in the riparian zone (median rank 29), substrate embeddedness (rank 28), slope (rank 26), and substrate matrix (rank 24).

The selected sets of variables for use in the discriminant models and their performance in predicting reference sites to the faunal groups are shown for the five data sets in Table 6. The selection of a final list of variables to be used in each of the models was determined by the model's ability to predict the reference sites to the group to which they actually belonged (Reynoldson et al. 1997). The family- and genus-assemblage and species-metric models performed similarly, predicting between 55.7 and 57.1% of the sites correctly using cross-validation. The species-assemblage model only predicted 42.0% of the sites correctly. All but the species-assemblage model performed similarly in predicting sites to the various groups, no group having <40% accuracy and most groups having >60% accuracy using resubstitution. However, in the species-assemblage model, three of the groups had <40% accuracy and one had only 16% accuracy (Table 6).

Eighteen of the 29 variables considered were used in the five models. The number of variables used ranged from eight to 11. The variables common across the models were longitude, ecoregion, and stream order, each of which was used in four models. Presence of grass in the riparian zone, width, substrate framework, and alkalinity were used in three of the models and bankfull width was used in four models. Examination of the complete list suggested that the faunal assemblages were structured by large-scale variables, such as location and stream size.

Assessment of test sites

The test sites were first predicted to one of the reference groups using each of the five predictive models, and sites were then assessed by comparing them with the appropriate reference-site group (Table 7). There was no a priori way of determining whether or not the test sites were actually impaired, but the sites were selected because of visible evidence of physical disturbance or human activity in the vicinity of the test site. Because there was also no a priori way of determining the correctness of taxonomic or metric classification, we examined the sensitivity and concordance among the assessments.

Concordance of the models was determined by similarity among the assessments of a test site (Table 7). At only two sites, SAL1 and TYA1, was there 100% concordance among the assessments. Four of the five assessments were the same at seven sites (NIC5, SAL2, SAL3, SAL4, WIL2, TOR10, and TYA5). At the other extreme, only two assessments were the same at three sites (GUI1, GUI3, and TYA2). Most sites (12) only showed a difference of one band. However, one site (GUI3) was assessed to each of the four bands by the different models. Three different assessments resulted at six sites (GUI1, WIL3, TOR11, TYA2, WIL1, and WIL4).

The sensitivity of the models was determined by the degree to which they detected the difference between a test site and the reference sites. In general, the family-level models, both assemblage and metric, were most sensitive in assessing test sites; only nine (family assemblage) and six (family metric) of the 21 sites were assigned to Band 1. The species-assemblage and species-metric models assigned nine and 10 sites, respectively, to Band 1. The family-assemblage model also assessed the most sites (six) as being in either Band 3 or Band 4. The species- and genus-assemblage models assessed four and three sites, respectively, to Bands 3 and 4, the family-metric model assigned two sites to these higher bands, and the species-metric model assigned one site.

An example of the model output for 10 test sites predicted as belonging to reference Group 7 from the species-assemblage model is shown in Fig. 3 for axes 2 and 3 of the ordination. Sites TOR11 and BOW13 are outside the 99% probability ellipse (Band 3) constructed around the reference sites and are assessed as different from reference. (The explanation for why BOW13 appears in Band 4 in Table 7 is given below.) These sites were exposed to logging activity. Site GUI3 (mining) is in Band 2 in Fig. 3 but is also assigned to Band 3 in Tables 7 and 8 (see explanation below). The three species characterising Group 7 (Table 4) were

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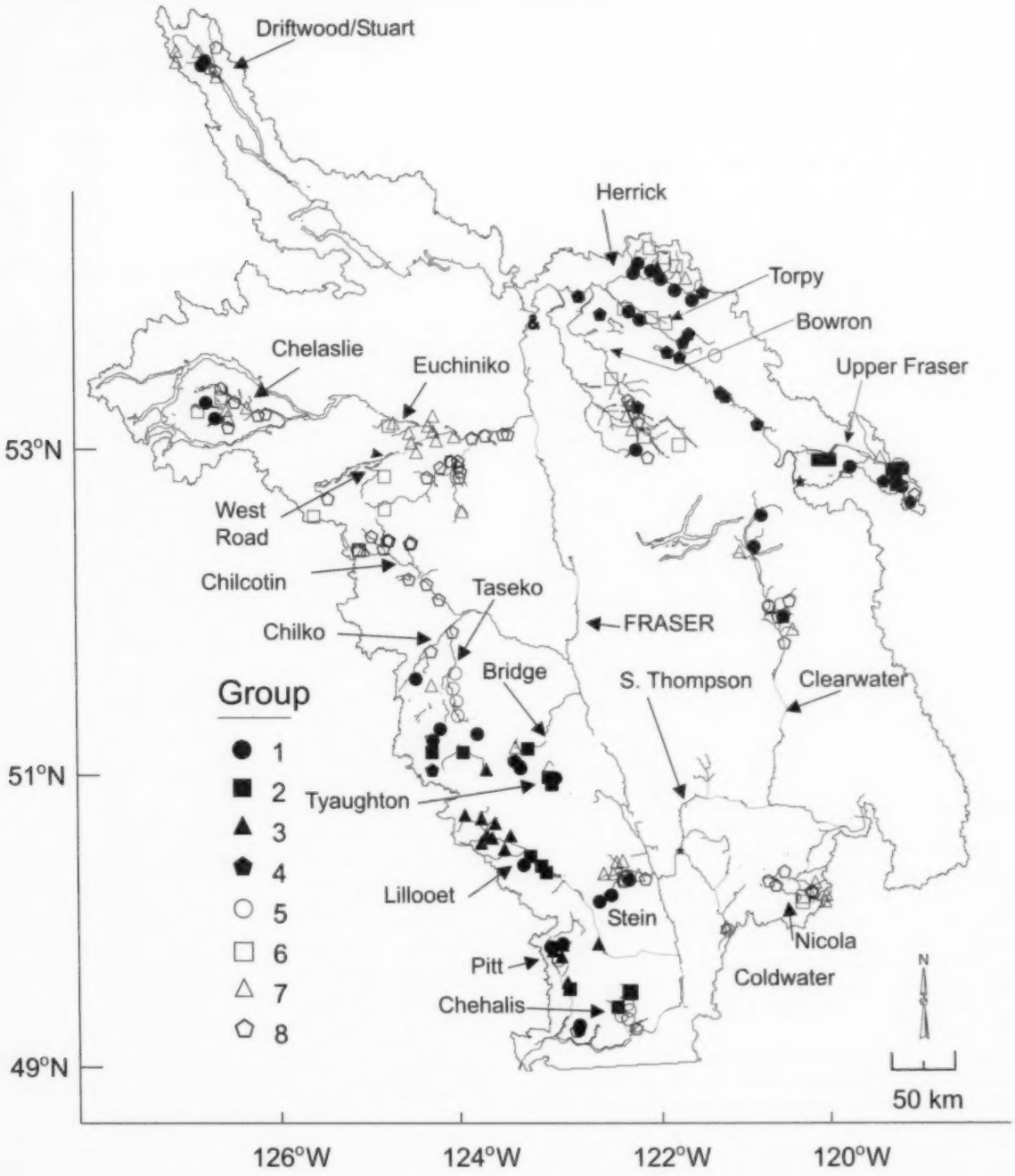
Fig. 2. Geographic distribution of eight groups formed from cluster analysis of invertebrate assemblage data at the species level from 219 reference sites in the Fraser River catchment.



Micropsectra spp., *Capnia* spp., and *Tvetania bavarica*, which were either absent or occurred in much lower numbers at these three sites compared with the reference sites (Table 8). Two other sites (DEA1 and TYA5) were in Band 2, outside the 90% ellipse (Fig. 3). *Micropsectra* spp. and *Capnia* spp. were either absent or present in low numbers at DEA1 (agriculture) and TYA5 (logging) compared with the reference sites (Table 8). However, DEA1 had a high total abundance compared with other Band 2 and 3 sites. The remaining test sites (NIC5, SAL1, TYA1, TYA2, and WIL4) were inside the 90% probability ellipse (Band 1) constructed around the reference sites, and therefore, these sites were

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Table 6. Summary of the performance of discriminant models used for three taxonomic levels and with two sets of metrics.

	Model				
	Species assemblage	Genus assemblage	Family assemblage	Species metric	Family metric
No. of taxa or metrics	124	97	74	9	8
No. of site groups	8	6	4	3[a]	4
No. of variables used in model	8 (LAT, LON, ECOR, SORD, WIDTH, BNKWL, GRASS, MNVEL)	11 (LON, ECOR, SORD, WIDTH, BNKWI, MNVEL, FWORK, EMBED, PH, ALK, COND)	9 (LAT, LON, ECOR, GRASS, WIDTH, MXDEP, FWORK, ALK, COND)	8 (LON, ECOR, ALT, SORD, MNDEP, BNKWI, SLOPE, FWORK)	8 (ALT, SORD, MCPHYT, GRASS, MXDEP, BNKWI, SLOPE, ALK)
Proportion of sites correctly predicted per group (resubstitution)					
Group 1	0.16	0.46	0.64	0.51	0.50
Group 2	0.35	0.67	0.60	0.66	0.42
Group 3	0.56	0.55	0.54	0.78	0.62
Group 4	0.50	0.70	0.67	na	0.69
Group 5	0.71	0.66	na	na	na
Group 6	0.35	0.62	na	na	na
Group 7	0.48	na	na	na	na
Group 8	0.54	na	na	na	na
Total sites correctly predicted (%)					
Resubstitution	43.8	61.2	61.6	61.2	55.3
Cross-validation	42.0	56.2	55.7	57.1	51.6

Note: The proportion of sites correctly predicted for each group and the total percentage of correctly predicted reference sites are given. Variable abbreviations as in Table 2. na, not applicable.

[a]A fourth group of one site was formed but discarded from further analysis.

equivalent to reference. These sites generally had greater numbers than the previous sites of the three taxa characteristic of Group 7 (Table 8), with numbers in the range observed at reference sites.

All sites in Bands 2 and 3 on the right side of the plot with high axis 2 scores (BOW13, TOR11, TYA5, and GUI3) had total numbers one or two orders of magnitude lower than reference. These sites were all associated with logging or mining. The impaired agricultural site (DEA1) had high total abundance and low axis 2 scores and was clearly discriminated from the logging sites in ordination space (Fig. 3).

The designation of GUI3 and BOW13 in Tables 7 and (or) 8 differed from that shown in Fig. 3. Site GUI3 was located in Band 2 on axes 2 and 3 (Fig. 3) but was in Band 3 on axes 1 and 2, so it was assessed as being in Band 3 in Tables 7 and 8. BOW13 was in Band 3 in Fig. 3, but this site was predicted to both Group 7 ($p = 0.492$) and Group 6 ($p = 0.276$). When assessed against the Group 6 reference sites, it was outside the 99.9% ellipse (Band 4) and was therefore assessed as Band 4 in Table 7.

Comparison of models

The performance of each of the five models based on seven attributes (sensitivity, robustness, usability, seasonal and annual variability, predictive performance, and model certainty) is summarised in Table 9. The family-assemblage model was most sensitive, based on the degree to which test sites were assessed as being different from reference, as described above. The family-metric model was the next most sensitive. The species (metric and assemblage) and genus-assemblage models were the least sensitive. This observation seems counterintuitive, but species models are likely biologically more noisy than family models. There tends to be more variation within a reference group at the species level because there are more taxa, most of which have low abundance. For example, at the family level, common taxa (present at >50% of sites) represented from 19.0 to 23.1% of all taxa, whereas at the species level the common taxa only represented between 3.0 and 8.5% of all the taxa found in a group. Rare taxa do not contribute as much information in multivariate methods as common taxa, so it takes a greater change to cause a response.

The family-metric model was the most robust. Nineteen of 21 sites were the same as the median assessment in the family-metric model compared with only 12 for the family-assemblage model (Table 7). In the family-assemblage model, all but one of those sites different from the median were assigned to a higher band, this being the most sensitive model in detecting difference from reference. Variation in the assessments for the species-assemblage, genus-assemblage, and species-metric models showed test sites to be almost equally divided between being more or less different from the reference group than the median.

Usability of the models is affected by taxonomic effort. More work is obviously required when identifying organisms to the species level. A second issue relates to the consistency of identifications. The reference-condition approach requires that samples from a test site be identified to the same level as samples from reference sites. Different levels of taxonomic resolution also result in serious data management problems. Last, the use of metrics requires an additional series of calculations to produce the derived measures, and there is some loss of information when using metrics.

Annual variability was greatest in the species-assemblage model; different assemblages occurred at the three sites sampled in each of three years. In contrast, at the family level (both assemblage and metric), two of the three sites remained members of the same faunal group over the three

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Table 7. Comparison of five predictive models in assessing 21 tests sites exposed to agricultural (A), mining (M), and logging (L) activity.

	Assemblage model						Metrics model				
	Species		Genus		Family		Species		Family		
Site	Prob	Band	Prob	Band	Prob	Band	Prob	Band	Prob	Band	Median band
DEA1 (A)	0.54	2	0.54	2	0.86	1	0.93	1	0.99	1	1
DEA2 (A)	0.72	1	0.41	2	0.91	2	0.91	1	0.99	1	1
DEA3 (A)	0.69	1	0.46	2	0.94	1	0.91	2	0.99	2	2
NIC5 (A)	0.58	1	0.79	1	0.86	1	0.73	1	0.84	2	1
SALT (A)	0.48	1	0.56	1	0.93	1	0.76	1	0.83	1	1
SAL2 (A)	0.64	1	0.65	1	0.82	1	0.91	2	0.89	1	1
SAL3 (A)	0.59	1	0.50	2	0.96	1	0.91	1	0.97	1	1
SAL4 (A)	0.61	2	0.69	3	0.97	2	0.94	2	0.99	2	2
GUI1 (M)	0.70	2	0.66	3	0.61	4	0.91	4	0.92	3	3
GUI3 (M)	0.66	3	0.56	1	0.48	4	0.62	2	0.92	2	2
WIL2 (M)	0.33	2	0.41	2	0.42	4	0.45	2	0.34	2	2
WIL3 (M)	0.36	2	0.53	3	0.44	2	0.42	1	0.56	2	2
BOW13 (L)	0.49	4	0.50	2	0.53	4	0.69	2	0.34	2	2
BOW14 (L)	0.45	2	0.55	1	0.38	2	0.42	2	0.36	2	2
TOR10 (L)	0.35	2	0.51	2	0.73	2	0.44	1	0.67	2	2
TOR11 (L)	0.30	3	0.48	2	0.76	3	0.42	1	0.89	2	2
TYA1 (L)	0.60	1	0.75	1	0.72	1	0.56	1	0.54	1	1
TYA2 (L)	0.41	1	0.85	2	0.97	3	0.82	1	0.52	2	2
TYA5 (L)	0.23	2	0.51	1	0.39	2	0.71	2	0.40	2	2
WIL1 (L)	0.46	3	0.50	2	0.51	1	0.42	2	0.44	2	2
WIL4 (L)	0.51	1	0.72	1	0.48	1	0.84	2	0.59	4	1
Sites assessed as:											
Band 1		9		8		9		10		6	
Band 2		8		10		6		10		13	
Band 3		3		3		2		0		1	
Band 4		1		0		4		1		1	

Note: The probability (Prob) of each site belonging to the matched reference group and the assessment band (1, equivalent to reference; 2, possibly different; 3, different; 4, very different) are presented. Test sites (rivers): BOW, Bowron, DEA, Deadman, GUI, Guichon, NIC, Nicola, SAL, Salmon, TOR, Torpy, TYA, Tyaughton, WIL, Willow.

years. The same trend was observed for the 11 sites examined for two years: nine and 10 sites in the family-metric and family-assemblage models, respectively, had the same faunal assemblage in both years, whereas only six sites were assigned to the same faunal groups using the species-assemblage model.

Reece et al. (2001) examined the effects of seasonal variation on the assessment of sites using genus- and family-assemblage models constructed from samples collected in autumn. Fifty-seven percent of reference sites sampled in the winter, spring, and summer were located inside Band 1 (90% probability ellipse) at the genus level compared with 48% at the family level. Thus, the family-assemblage model was more sensitive than the genus-assemblage model to seasonal variation. However, if Bands 1 and 2 are considered together, the sensitivity of both models was the same (87%; see Reece et al. 2001, their table 2).

The last two factors used to assess the five models related to their ability to predict sites to faunal groups. The prediction of the reference sites is summarised by cross-validation accuracy (Table 6). The species-metric, genus-assemblage, and family-assemblage models performed similarly well (55.7–57.1% accuracy). However, the species-assemblage model performed poorly (42%) and was ranked lowest. Last, the certainty with which the models assigned test sites to a faunal group was compared by using the average of the probabilities of group membership from the 21 test sites (Table 7). The family-assemblage, species-metric, and family-metric models performed the best (Table 9).

Discussion

Hawkes (1975) identified the value of a biological classification system that could be coupled to a system that used physical and chemical features for predicting the type of macroinvertebrate assemblage that occurred in lotic systems. Wright et al. (1984) subsequently published a classification of running-water sites, which was the first application of predictive modelling of invertebrate community structure to running waters and which was the genesis of the River Invertebrate Prediction and Classification System (RIVPACS) approach for water-quality monitoring now being used in the United Kingdom. Our study was designed to provide a similar scheme for the assessment of aquatic ecosystem quality for the Fraser River catchment in British Columbia, based on predictive models of invertebrate assemblages.

Comparison of Fraser River models

There are two current major themes in regional biomonitoring programmes. There has been considerable debate

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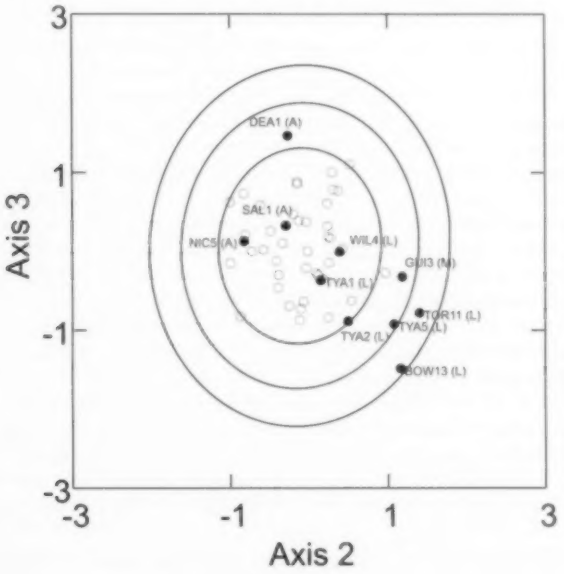
Table 8. Mean (±SD) total abundance (number per 3-min kicknet sample) and mean (±SD) abundance (number per 3-min kicknet sample) of taxa characteristic of reference Group 7.

	Assessment band (Group 7)	Abundance			
		Total	*Micropsectra* spp.	*Capnia* spp.	*Tvetania bavarica*
Reference		12 207 (7658)	1627 (1379)	695 (1441)	336 (701)
Test site					
TOR11	3	1 736	9	0	0
BOW13	3	780	27	27	20
GUI3	3	1 307	0	43	0
DEA1	2	21 300	0	0	500
TYA5	2	1 667	22	33	222
NIC5	1	23 200	5300	3500	1800
SAL1	1	10 000	2700	650	400
TYA1	1	9 200	1500	400	450
TYA2	1	2 350	67	317	33
WIL4	1	9 200	1550	50	100

Note: Test sites (rivers): BOW, Bowron; DEA, Deadman; GUI, Guichon; NIC, Nicola; SAL, Salmon; TOR, Torpy; TYA, Tyaughton; WIL, Willow.

Fig. 3. Assessment of 10 test sites (solid circles) predicted as belonging to reference Group 7 from the species-assemblage model showing two ordination axes. The test sites were exposed to agricultural (A), logging (L), and mining (M) activities. Probability ellipses are calculated at the 90, 99, and 99.9% probability levels around reference sites (open circles) only. Test sites (rivers): BOW, Bowron; DEA, Deadman; GUI, Guichon; NIC, Nicola; SAL, Salmon; TOR, Torpy; TYA, Tyaughton; WIL, Willow.



in the literature (e.g., Gerritsen 1995; Norris 1995) regarding the merits of the multivariate modelling approach using species abundance or presence (e.g., RIVPACS in the United Kingdom; Wright et al. 1984) versus the multimetric approach (e.g., Rapid Bioassessment in the United States; Resh and Jackson 1993). In this paper, part of our objective was to incorporate the predictive capacity of multivariate methods with the ecological comprehension included in multimetrics and to examine the performance of this hybrid approach.

For the Fraser River catchment, five models using three taxonomic levels and two sets of metrics were created from 219 sites to describe expected benthic assemblages. We have attempted to be as objective and quantitative in our assessment of the models as possible using different attributes. The overall performance of the five models in assessing the effects of various human activities on the invertebrate community indicated that the family taxonomic level provided better clarity than species or genus. The incorporation of metrics provided little extra value, and therefore, we recommend the use of the family-assemblage model for biomonitoring in the Fraser River catchment because it is clearly the most sensitive and least variable. Its overall performance was similar to that of the family-metric model, it avoids an extra calculation step, and, most importantly, it was best able to detect differences from reference. If, however, the objective of the study is an assessment of species expected to occur at a site, as used in the RIVPACS approach (Wright 1995) or for conservation or biodiversity studies, then the species-assemblage model should be used. The species- and family-assemblage models should only be used on samples collected in autumn from the Fraser River catchment because these models are sensitive to seasonal variation.

Comparison with other regional models

The premise behind predictive models of benthic community structure is that there is a relationship between taxa present and environmental conditions at a site. DFA has been used for two decades as a method to relate environmental variables and invertebrate community structure (Green and Vascotto 1978). In its first large-scale application, Wright et al. (1984) achieved 76.1% success in the prediction of 268 sites to 16 groups with 28 environmental variables. Other authors have had similar success, with correct

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Table 9. Comparison and ranking of five predictive models for assessing benthic invertebrates, ranked from 1 (best) to 5 (worst) based on seven characteristics.

	Model				
	Species assemblage	Genus assemblage	Family assemblage	Species metric	Family metric
Sensitivity (summed score in parentheses)	3 (38)	3 (37)	1 (43)	5 (34)	2 (39)
Robustness (no. of sites same as median)	3 (13)	3 (13)	5 (12)	2 (14)	1 (19)
Usability (low, medium, or high)	4 (low)	2 (medium)	1 (high)	5 (very low)	2 (medium)
Annual variability (sites with same assemblage in multiyears)	5 (6)	2 (11)	1 (12)	4 (9)	2 (11)
Seasonal variability (% sites not assessed as reference)[a]	nd	Medium	Medium	nd	nd
Predictive performance (cross-validation, %)	5 (42.0)	2 (56.2)	3 (55.7)	1 (57.1)	4 (51.6)
Model certainty (average p level for 21 test sites)	5 (0.51)	4 (0.58)	2 (0.70)	2 (0.70)	1 (0.71)
Overall rank (sum of ranks)	25	16	13	19	12

Note: Ties were allowed. nd, no data.
[a]Not ranked because only two models were assessed.

predictions ranging from 55.9% (this study) to 79.6% (King 1981). The species-assemblage model for the Fraser River catchment is in the lower range of predictive performance. We suspect two reasons for the lower performance in the Fraser River catchment. First, the success of model prediction tends to decline as the number of sites increases (Wright 1995) because discrete assemblages are less likely to be found as the number of sites increases and the distributional continua of taxa are incorporated into the database. Second, the Fraser River catchment is less species rich than some other regions.

The effect of increasing number of sites on reducing prediction accuracy is somewhat counterintuitive. However, this effect is illustrated by successive family-assemblage models constructed for the Fraser River. With 1994 data for 41 sites (four groups), five predictor variables correctly predicted 74.4% of the sites (Reynoldson et al. 1997). Models developed using 1994 and 1995 data with 10 variables correctly predicted 63.0% of 127 sites to five groups (Rosenberg et al. 2000). In this paper, with 219 sites, the model correctly predicted 55.7% (cross-validation) of the sites. A similar decline in the percentage of correctly predicted sites has been observed in the United Kingdom as their data set has increased from 268 to 438 to 614 reference sites (Reynoldson and Wright 2000). The explanation for this apparent contradiction is rooted in the use of DFA for predicting the invertebrate assemblages. DFA requires the classification of reference sites into groups based on the invertebrate fauna. However, ordination of each of the five invertebrate data sets for the 219 reference sites on the Fraser River failed to identify clearly distinct groups of sites. A similar observation was made by Wright et al. (1984) in their classification of 268 sites in the United Kingdom. Wright et al. (1984) explained that such a result was to be expected because physical and environmental gradients occur along river systems and favour progressively changing assemblages of organisms (e.g., Vannote et al. 1980). Data from the Fraser River catchment also suggested continua of taxa distributions rather than sharp discontinuities, which is one of the problems associated with using classification and discriminant analysis for forming groups and predicting group membership. Because of the lack of natural discontinuities between sites, any classification is somewhat arbitrary.

The second reason for the low predictive performance of the models for the Fraser River may be the comparative paucity of the fauna. Low diversity would affect the ability to form distinct groups and thus make differentiation among groups more problematic. For example, Wright et al. (1984) recorded 599 taxa in just over 100 families from 268 reference sites in the United Kingdom, which has an area similar to that of the Fraser River catchment. The United Kingdom taxa count is almost double that observed from the Fraser River (318) from a similar number of families (74), and the United Kingdom is known to be species poor compared with continental Europe because of the last glaciation (Reynoldson 1983). In contrast, Parsons and Norris (1996) recorded 56 families from just 46 reference sites in one catchment in Australia. It is noteworthy that the number of biological groups (seven species groups) formed from the Fraser River data set is much lower than that of the United Kingdom (16 species groups), with similar numbers of sites over a similar area. The relative paucity of the Fraser River fauna results in less differentiation among the groups and could be compounding reduced accuracy in the models.

Implications of misclassification to the predictive models

The recommended model for the Fraser River had a cross-validation error rate of 44.3%. The probability of 21 test sites belonging to reference groups ranged from a low of 38% to a high of 97%, with the average being 70%. The fact that there is uncertainty in assigning a site to a biotic group raises a question about the confidence that users should have in using this assessment approach. The RIVPACS method circumvents some of the uncertainty problems associated

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with classifying to groups, and the consequent error with the predictive models, by weighting the prediction of the expected fauna at a test site by the probability of the test site belonging to each of the reference site groups (Wright 1995). However, this approach only uses presence–absence data. In our view, the use of variation in abundance, which is incorporated in ordination of counts, is helpful in distinguishing impaired sites from reference sites. The prediction error partly results from similarities among the groups and the imposition of groups upon the continuum of species distributions. Examination of the reference sites shows considerable similarity among some groups. From the construction of 90% probability ellipses around each reference group, we determined the number of reference sites from other groups falling within each reference group. There is considerable similarity between some of the groups, (e.g., 82.5% of the Group 1 sites fall within the Group 2 90% probability ellipse). In contrast, none of the Group 1 sites fall within the Group 4 ellipse, none of the Group 2 sites fall within the Group 3 or Group 4 ellipse, and none of the Group 4 sites fall within the Group 1 ellipse. Examination of the results of using the model on 21 test sites showed that 10 had a >25% probability of belonging to more than one reference group, and in all cases, these were predicted to groups where there was considerable overlap with another reference group (data not shown). Therefore, the consequence of a site being incorrectly assigned is that there is still a large number of reference sites in the appropriate ordination space. However, this overlapping classification is a limitation of the method being used and a consequence of the requirement to impose groups upon the community continuum. Whether the RIVPACS or benthic assessment of sediment (BEAST) method is used, it is critical to apportion the variability of the reference site assemblages so that test sites are compared with appropriate reference sites. As long as this step is consistently done and is appropriate to the intended use, then the specifics of the classification are probably not critical.

Alternative methods are under investigation to circumvent the need to form community groups. One approach (D.P. Faith, CSIRO, Canberra, Australia, personal communication) uses the entire reference data set and predicts the expected location of a site in the reference site cloud. Distance from the predicted location in ordination space is used as an indicator of the stress being observed at a test site.

In conclusion, the classification of reference sites for the Fraser River catchment should provide a valuable tool for broad application in environmental assessment. In reality, environmental assessment and an adequate description of the response to pollution are almost always a compromise between the scientific ideal and political, financial, and logistic limitations (Warwick 1993). Ongoing work is extending the database and models to the Lower Fraser River. The software for the Fraser River catchment will soon be widely available, incorporating the reference data and predictive models for use by government, industry, and others.

Acknowledgements

This study was made possible by funding from FRAP. Special thanks to Taina Tuominen for her unflagging support, which allowed the study to happen. We thank Craig Logan and Scott Hughson for sorting and identifying specimens. Mike Mawhinney, Sherri Thompson, and the pilots of Canadian Helicopters made the study possible. We also thank Jordan Rosenfeld, Gary Sprules, and an anonymous reviewer for their comments, which substantially improved the manuscript.

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Implications of seasonal variation for biomonitoring with predictive models in the Fraser River catchment, British Columbia

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Abstract: Reference-condition models for the Fraser River catchment were developed using samples collected during the autumn of 1994, 1995, and 1996. The goal of this study was to examine applicability to the reference-condition models of samples collected in other seasons and the effect of taxonomic resolution (genus and family) on model sensitivity to seasonal variation in the benthic invertebrate assemblage. Samples from eight streams representing interior, coastal, and large-river habitats were collected in spring, summer, autumn, and winter of 1995 and in spring of 1996. The benthic invertebrate assemblage changed seasonally such that the models could not be used for seasons other than autumn. The models were equally sensitive to seasonal variation when genus-level or family-level data were used. We recommend that test samples (i.e., samples collected from disturbed sites and meant for comparison with the reference database) be collected either during the autumn or over multiple sampling dates to reduce the possibility that seasonal shifts or stochastic events will lead to erroneous conclusions about the state of a test site.

Résumé : Des échantillons recueillis aux automnes 1994, 1995 et 1996 ont servi à élaborer des modèles avec conditions de référence dans le bassin hydrographique du fleuve Fraser. Les buts de l'étude sont de vérifier si des échantillons prélevés en d'autres saisons peuvent être appliqués aux modèles avec conditions de référence et d'examiner les effets du degré de résolution taxonomique (genre et famille) sur la sensibilité des modèles à la variation saisonnière de la communauté des invertébrés benthiques. Des échantillons ont été prélevés dans huit cours d'eau représentant des habitats de la côte, de l'intérieur des terres et des grandes rivières, au printemps, à l'été, à l'automne et à l'hiver 1995 et au printemps 1996. Les changements saisonniers de la communauté d'invertébrés benthiques sont tels que les modèles ne peuvent être utilisés qu'à l'automne. Les modèles restent aussi sensibles à la variation saisonnière, que les données soient identifiées au genre ou à la famille. Nous recommandons donc que les échantillons d'essai (i.e. les échantillons provenant de sites perturbés destinés à être comparés aux données de référence) soient récoltés à l'automne ou alors à plusieurs périodes durant l'année pour minimiser la possibilité que des changements saisonniers ou des événements aléatoires mènent à des conclusions erronées sur l'état du site à analyser.

[Traduit par la Rédaction]

Introduction

The reference-condition approach to river biomonitoring uses data on benthic invertebrate assemblages and associated physical, chemical, and biological conditions from a set of minimally impacted or reference sites to predict the expected benthic assemblage at possibly stressed test sites (Reynoldson et al. 1997). If a test-site assemblage falls within the range of variability found at reference sites with similar environmental conditions, the site is considered equivalent to reference. If the test site falls outside of the range, it is considered different from the reference condition. Accurate predictions of expected benthic assemblages are limited to the range of variability included within the reference database, which may or may not include seasonal variability.

Benthic communities change seasonally (Hynes 1970; Boulton and Lake 1992; but see Death 1995), but the implications for biomonitoring have not been fully established. Furse et al. (1984) recommended seasonal collection of reference samples when using predictive models. Their use of a reference data set that combined seasonal data for each site increased prediction accuracy of test sites. However, the additional time and cost of collecting and identifying samples from a large number of reference sites over several seasons are significant considerations that constrain the scope of biomonitoring programs with limited resources. Therefore, the implication of seasonal changes in the benthic community to the application of the reference-condition approach needs to be established.

Received March 22, 2000. Accepted March 31, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 12, 2001.
J15675

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 DOI: 10.1139/cjfas-58-7-1411 © 2001 NRC Canada

The purpose of this study was to determine the effect of seasonal changes in benthic invertebrate assemblages on the accuracy of predictions made with the BEnthic Assessment of SedimenT (BEAST) predictive model (Reynoldson et al. 1995). The model has been developed for bioassessment in the Fraser River catchment, Canada (Reynoldson et al. 2001). Specifically, we tested the effect of seasonal variation on the assessment of samples collected outside of the autumnal reference-sample period.

A second goal of this study was to determine the effect of taxonomic resolution (genus versus family) on the sensitivity of the model to seasonal variation. Seasonal variation should be manifest primarily at the genus level because representatives of families are likely to be present throughout the year. The most suitable level of invertebrate identification for biomonitoring depends on the study and the questions being asked (Resh and McElravy 1993). Zamora-Muñoz and Alba-Tercedor (1996) found that the family level of identification was sufficient for monitoring water quality in streams, but species data were required to determine the exact biological responses to stress. Monitoring at the family level is used by the Australian River Assessment Scheme (AusRivAS) and has been recommended for marine (Warwick 1993) and lake (Jackson and Harvey 1993) ecosystems.

Methods

Study sites

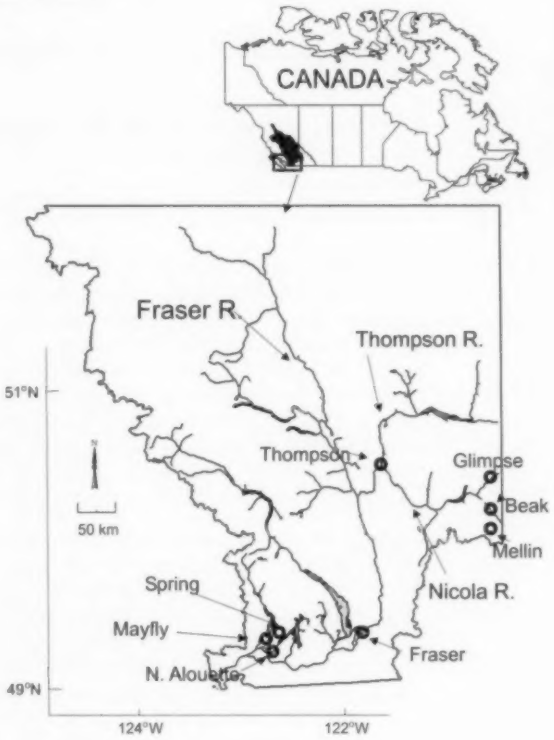
To ensure that the results of this study applied to streams from different ecoregions and to small streams as well as large rivers, seasonal change in assemblage structure was assessed for eight streams. This study was limited to eight streams for logistical reasons. All eight streams are located in the Fraser River catchment (Fig. 1) and include three continental streams (Mellin, Glimpse, and Beak creeks), three coastal streams (Spring Creek, Mayfly Creek, and the North Alouette River), and two large-river sites (Fraser and Thompson rivers). These study sites will be referred to as seasonal test sites. Six of the streams used as seasonal test sites were considered reference sites because they were not visibly disturbed, and their autumnal data were incorporated in the reference database used in developing the predictive models described in Reynoldson et al. (2001). However, during sample collection, it was decided that the Fraser River and Mellin Creek sites were possibly impaired. As a result, they were treated as disturbed sites for data analysis.

A detailed description of the study sites along with a discussion of the spatial variation of the benthic assemblage can be found in Reece and Richardson (2000). However, a few details of the study sites that highlight differences between the stream types are given here.

Continental climate streams receive very little precipitation through the summer, and highest discharge occurs in the spring as a result of snowmelt. Air temperatures range from 35°C in the summer to –30°C in the winter. These are hardwater streams with high alkalinity, high conductivity, and a slightly basic pH (Table 1). Agriculture is a dominant land use in continental regions of B.C. Mellin Creek was heavily used by cattle in the autumn and was therefore treated as a disturbed site and excluded from the reference database. Beak Creek was inaccessible in the winter.

The coastal climate streams receive heavy winter rains and correspondingly high and variable winter discharges. Air temperatures can range from 30°C in the summer to –10°C in the winter. The streams have soft water, low alkalinity, low conductivity, and are slightly acidic (Table 1).

Fig. 1. Location of sampling sites in southwestern British Columbia. All sampling sites (O) are located in the Fraser River catchment.



The two large-river sampling sites were the Thompson River at Spences Bridge and the Fraser River at Agassiz. Air temperatures at these sites range from 30°C in the summer to –20°C in the winter. The Fraser and the Thompson rivers have intermediate alkalinity and conductivity and pH similar to the those of the interior streams (Table 1). Land use around Spences Bridge and Agassiz consists of agriculture, some rural development, and forestry. There are major urban centers and pulp mills upstream of both sampling sites. Long-term studies on the invertebrate assemblage at Spences Bridge have indicated that the Thompson River is not heavily impacted at this point (J. Culp, Environment Canada, National Hydrology Research Institute, Saskatoon, Saskatchewan, personal communication), so it was considered suitable for inclusion in the reference database. The state of the Fraser River at Agassiz was unknown, so it was treated as a disturbed site and was excluded from the reference database.

Sample collection

The purpose of this study was to test the implications of seasonal variation on the use of predictive models created for biomonitoring in the Fraser catchment, so the same sample collection techniques were used as for collection of the reference database (Reynoldson et al. 2001). However, samples were collected over five seasonal sampling dates: late spring, summer, autumn, and winter of 1995 and early spring of 1996. The autumnal sampling date corresponded with the timing of the 1994 to 1996 collections of reference samples from throughout the Fraser River catchment (Rosenberg et al. 1999).

Benthic invertebrate samples were collected from riffles using kicknets (400-µm mesh). In the large rivers, kicknet samples were

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Table 1. Physical and environmental characteristics for each study stream.

	Stream class							
	Continental			Coastal			Large rivers	
	Mellin	Glimpse	Beak	Spring	Mayfly	N. Alouette	Fraser	Thompson
Latitude (N)	50°7′1.1″	50°15′2″	50°6′45.4″	49°16′0.3″	49°19′02″	49°17′0.8″	49°12′20.2″	50°25′28″
Longitude (W)	120°6′28.8″	120°14′9″	119°58′51″	122°34′0.4″	122°32′0.4″	122°32′0.6″	121°46′7.2″	121°19′35.3″
Elevation (m asl)	1123.1	1171.1	1003	132.9	413.5	315	68.7	204.2
Drainage basin (km^2)	52.35	10.18	86.41	1.99	2.14	9.58	217000	54900
Channel slope ($m \cdot m^{-1}$)	0.0204	0.0025	0.0170	0.0319	0.0020	0.0400	0.0002	0.0102
Channel width (m)	0.15–5.8	1.3–2.8	6.8–13.42	3.1–8.7	2.9–3.84	3.8–15	300–400.9	70–235.7
Mean depth (m)	0.07–0.41	0.08–0.22	0.106–0.27	0.03–0.99	0.11–0.88	0.21–0.38	0.4–1	0.3–0.5
Max. velocity ($m \cdot s^{-1}$)	0.09–0.93	0.07–1.18	0.15–1.06	0.23–0.29	0.08–0.67	0.43–1.01	0.225–1.72	0.152–1.41
Discharge ($m^3 \cdot s^{-1}$)	0.006–1.44	0.004–0.31	0.047–1.405	0.04–0.3	0.04–0.52	0.436–1.14	1060–4480	409–1630
Temperature (°C)	0.1–14.5	0.1–8.5	0.1–11.5	3.8–10	2–10	2–11	0–17.5	0.5–18
pH	7.21–8.1	7.69–8.25	7.44–8.45	6.37–6.73	5.71–7.68	5.65–6.68	6.94–8.08	7.58–8.65
Conductivity ($\mu S \cdot cm^{-1}$ at 25°C)	72.1–262.7	234.4–534.9	75.7–234.2	16.4–30	15.22–24.2	13–21.23	95.6–218	78.5–110.6
Alkalinity ($CaCO_3$) ($mg \cdot L^{-1}$)	40.2–97.6	123–201	30.2–86	4.9–12.1	2.4–10.2	0.1–4.5	39.2–56.9	29.2–42.2
NO_3NO_2–N ($mg \cdot L^{-1}$)	0.005–0.071	0.005–0.057	0.005–0.06	0.032–0.199	0.036–0.1	0.096–0.147	0.005–0.156	0.032–0.148
TKN ($mg \cdot L^{-1}$)	0.487–0.674	0.286–0.34	0.21–0.48	0.03–0.19	0.04–0.092	0.037–0.075	0.118–0.39	0.069–0.127
Total suspended solids ($mg \cdot L^{-1}$)	4.33–32.9	1.35–3.05	1.56–3.56	0.38–2.2	0.29–1.76	0.06–1.2	9.46–62.51	0.96–3.41
Total phosphorous ($mg \cdot L^{-1}$)	0.045–0.089	0.007–0.016	0.028–0.034	0.001–0.005	0.002–0.006	0.000–0.004	0.028–0.101	0.006–0.017

Note: Ranges are given for variables that change seasonally. TKN = total Kjeldahl nitrogen, asl = above sea level.

taken from the river edge proceeding into the river channel, whereas the small-stream samples were collected by zigzagging between stream banks. Samples were preserved in 4% buffered formaldehyde.

One-minute kicknet samples were collected at each site and date. Three samples per site per date were sorted and identified, and the data were pooled so that the data used represented invertebrate abundance per 3-min kicknet sample. If a sample contained <500 invertebrates, the entire sample was sorted and all invertebrates were identified. Samples containing >500 invertebrates were subsampled (Marchant 1989) and at least 200 animals were removed (Rosenberg et al. 1999). Organisms were identified to the lowest practical taxonomic level, usually genus and species. However, Ostracoda, Turbellaria, and Copepoda were not identified beyond class. Identifications were verified by experts (when possible), and a voucher series was deposited in the Royal British Columbia Museum, Victoria.

Forty environmental variables, including geographic, site, and channel characteristics and water chemistry, were measured either when the benthic samples were collected or from maps. The environmental variables measured were the same as those collected for the parent study (Rosenberg et al. 1999; Reynoldson et al. 2001).

Data analysis

Invertebrate abundance data were analyzed at both genus and family levels (exceptions listed above) to determine the sensitivity of the assemblage to seasonal changes. Invertebrate abundance data were used to test the implications of seasonal variation on the predictive model because abundance data were used in the creation and implementation of the model. Abundance data creates more sensitive models than presence–absence data (Armitage et al. 1987; Smith et al. 1999). Genus level was used because not all larvae could be identified to species. Identification to family is time and cost efficient, achievable for most taxa, and can be consistent among laboratories. Both genus and family data sets and reference groups used for the analysis were the same as those used in Reynoldson et al. (2001). Rare taxa (occurrence at <5% of sites) were removed from the genus data set because they create noise that obscures patterns in classification analysis (Gauch 1982). No taxa were removed from the family data set. The spatial organization of habitat attributes and biological responses was addressed in Reynoldson et al. (2001).

We wanted to determine whether the seasonal test samples were different from the autumnal reference condition as defined by Reynoldson et al. (2001), thus resulting in Type I errors (i.e., a site being classified as impaired when it was not). To test the model with seasonal data, seasonal samples were compared with the autumnal sampling from each seasonal test site using the reference groups defined by Reynoldson et al. (2001), ordination, and probability ellipses. The extent of seasonal variation could only be assessed by comparison with the autumnal reference sites because they were the only sites with a known condition.

To compare the seasonal test samples with the reference condition, the reference group to which each site belonged was determined using cluster analysis. The variability of the seasonal samples relative to the reference sites included in the reference group could then be established. Variability of ordination scores, used to assess the seasonal variation of the test sites, was assessed using probability ellipses. Details of the data analysis techniques used are given below.

Cluster analysis (agglomerative hierarchical fusion with unweighted pair group mean averages, UPGMA) of the faunal data from the reference database produced reference groups (Reynoldson et al. 2001). The autumnal samples collected at the six unimpacted seasonal test sites were included in the cluster analysis and thus were included in the reference groups. The Fraser River catchment model (Reynoldson et al. 2001) was used to classify the Fraser River

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and Mellin Creek sites to reference groups defined by the model because these sites appeared disturbed and were therefore considered not equivalent to reference.

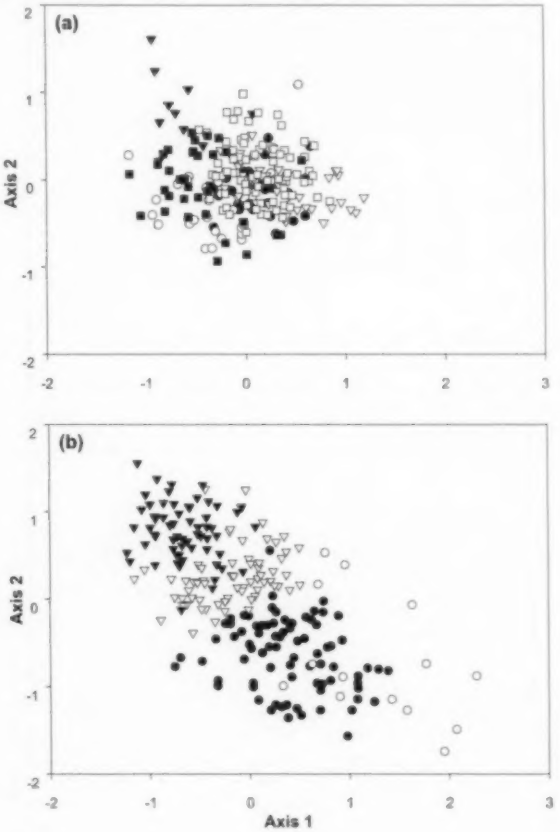
To determine the absolute seasonal change in the benthic assemblage, seasonal faunal data for each test site were ordinated (semi-strong hybrid multidimensional scaling, HMDS, Belbin 1991) with the reference group to which the seasonal test site was assigned based on the autumnal sampling. Gaussian bivariate probability ellipses (90%, 99%, and 99.9%) were calculated and plotted using the ordination scores of only the reference-site data in each group (SYSTAT 1990, Proc Scatterplot). The location of the seasonal test sites in the four bands created by the probability ellipses was examined and used to establish whether the seasonal samples could be assessed as equivalent to reference (Reynoldson et al. 2001).

The use of probability ellipses and the bands that they create allows the difference between a test site and the reference community to be categorized. Invertebrate assemblage responses can then be viewed along a gradient of impact responses. The level of departure from the reference condition that constitutes unacceptable impairment is ultimately a subjective decision. The choice of the 90% probability ellipse as the first band (Band 1) is based on previous water-quality studies (Wright 1995) and a desire to reduce the potential of making Type II errors (classifying a site as not different from the reference condition when it is). Note that the probability bands define the Type I error. There is no other way of proportionally assigning levels of impairment, so 99% and 99.9% probability ellipses were selected that created stress bands (Bands 2, 3, and 4) of equal widths. Sites within the 90% ellipse (Band 1) are considered to be equivalent to reference. Sites between the 90% and 99% probability ellipses (Band 2) are considered to be possibly different from reference because there is a 10% chance that sites will fall in this band as a result of normal variability (Type I error rate). Sites between the 99% and 99.9% probability ellipses (Band 3) are considered different from reference because there is only a 1% chance that the sites will be incorrectly described as different. Sites that fall outside of the 99.9 % probability ellipse (Band 4) are considered to be very different from reference sites (Reynoldson et al. 2001).

Results

Cluster analysis of the reference data set resulted in six groups being formed for the genus level (97 taxa) and four groups for the family level (74 taxa) (Reynoldson et al. 2001). The most frequently occurring taxa in each reference group are listed in Reynoldson (et al. 2001). Ordination of the reference data showed the location of the six groups in ordination space for the genus level (Fig. 2*a*) and four groups for the family level (Fig. 2*b*). The reference-site groups to which the cluster analysis assigned the seasonal test sites, based on the autumnal data, are summarized in Tables 2 and 3. At the genus level, the cluster analysis placed the autumnal samples from the six unimpacted seasonal test sites into Groups 2 and 5. Mayfly Creek, Spring Creek, the North Alouette River, and the Thompson River samples had generally low invertebrate abundance and were included in Group 2. The continental streams (Glimpse and Beak) had high invertebrate abundance and were placed into Group 5. Of the two potentially stressed sites, the Fraser River site (intermediate in abundance between groups 2 and 5) was predicted to Group 4 and Mellin Creek was predicted to Group 5 based on the autumnal samples. A detailed description of the invertebrate composition at the seasonal test sites can be found in Reece and Richardson (2000).

Fig. 2. Ordination of Fraser River catchment reference sites based on invertebrate data: (*a*) genus identification level and (*b*) family identification level. Sites were assigned to respective groups by cluster analysis: Group 1, solid circles; Group 2, open circles; Group 3, open triangles; Group 4, solid triangles; Group 5, open squares; Group 6, solid squares.



At the family level, classification and prediction of seasonal test sites resulted in the sites being spread across all four reference groups (Table 2). The coastal streams were classified into Group 1. The Thompson River was predicted to Group 2. Of the continental streams, Glimpse Creek was placed into Group 4 and Beak Creek was placed into Group 3. Of the two exposed sites, Mellin Creek was assigned to Group 4 and the Fraser River was assigned to Group 2 (Table 3). When tested, the sites were consistently predicted to the same group using environmental measurements taken at different seasons, which suggested that the predictive model of group membership based on environmental variation was robust and not sensitive to seasonal variation in habitat predictors.

Locations of the seasonal test sites in the ordination space of the group to which they were classified are summarized in Table 2 for the reference sites and Table 3 for the exposed sites. A seasonal test-site sample located within the 90% probability ellipse (Band 1) for all axes was considered the same as the reference condition. A seasonal test-site sample that fell outside of the 90% ellipse (Bands 2, 3, or 4) for any

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Table 2. Summary of the groups into which the seasonal test sites were classified, based on the autumnal sampling and where the seasons fell in the probability ellipses of the ordination space.

Streams			Genus		Family	
Location	Study site	Season	Faunal group	Band	Faunal group	Band
Continental	Glimpse	Autumn 1995	5	1	4	2
		Spring 1995	5	4	4	3
		Summer 1995	5	4	4	2
		Winter 1995	5	2	4	2
		Spring 1996	5	2	4	2
	Beak	Autumn 1995	5	1	3	2
		Spring 1995	5	2	3	1
		Summer 1995	5	2	3	1
		Spring 1996	5	1	3	1
Coastal	Spring	Autumn 1995	2	1	1	1
		Spring 1995	2	1	1	2
		Summer 1995	2	2	1	3
		Winter 1995	2	1	1	2
		Spring 1996	2	1	1	2
	Mayfly	Autumn 1995	2	2	1	1
		Spring 1995	2	1	1	1
		Summer 1995	2	2	1	3
		Winter 1995	2	1	1	2
		Spring 1996	2	1	1	1
	N. Alouette	Autumn 1995	2	1	1	1
		Spring 1995	2	1	1	1
		Summer 1995	2	1	1	1
		Winter 1995	2	1	1	1
		Spring 1996	2	1	1	1
Large	Thompson	Autumn 1995	2	2	2	1
		Spring 1995	2	2	2	2
		Summer 1995	2	1	2	1
		Winter 1995	2	1	2	1
		Spring 1996	2	3	2	2
	Autumnal samples	Band 1		4 (67%)		4 (67%)
		Band 2		2 (33%)		2 (33%)
	Non-autumnal samples	Band 1		13 (57%)		11 (48%)
		Band 2		7 (30%)		9 (39%)
		Band 3		1 (4%)		3 (13%)
		Band 4		2 (9%)		0

Note: See Fig. 3 for a visual placement of the probability ellipse bands: Band 1, within the 90% probability ellipse; Band 2, between the 90% and 99% probability ellipses; Band 3, between the 99% and 99.9% probability ellipses; Band 4, outside of the 99.9% probability ellipse.

pair of ordination axes was considered to be different from reference. Thus any conclusions as to the state of a seasonal test site were conservative.

Each seasonal test-site benthic assemblage changed seasonally, in ordination space, in different directions, and with different magnitudes at both the genus and family levels. These seasonal changes caused some seasonal test-site samples to fall outside of Band 1 (Fig. 3, Table 2). At the genus level, all sites except the North Alouette River had sampling dates that fell outside of Band 1 (some sampling dates for Glimpse Creek fell in Band 4, Table 2). These sites were not visibly disturbed but could be considered different from the reference condition outside of the reference sample season. At the genus level, 57% of the non-autumnal samples were assessed as equivalent to reference (Band 1, Table 2), 30% were assessed as possibly different from reference (Band 2), and the remaining 13% were different to very different from reference.

At the family level, 48% of the non-autumnal samples were in Band 1 (Table 2), 39% were classified as Band 2, and 13% were classified as Band 3. Therefore, seasonal changes in the invertebrate assemblage affected the location of a stream in ordination space, but the results changed with each stream and taxonomic level.

For the disturbed sites, we have shown the concordance between the autumnal assessment of the sites based on the discriminant function analysis (DFA) classification of the sites and the assessment based on sampling in other seasons. Concordance ranged from 0% to 75% and was lower at the genus level than at the family level (Table 3).

Discussion

Seasonal change at the reference sites

Seasonal changes in invertebrate assemblages can be large in some systems (Hynes 1970; Furse et al. 1984) or can be

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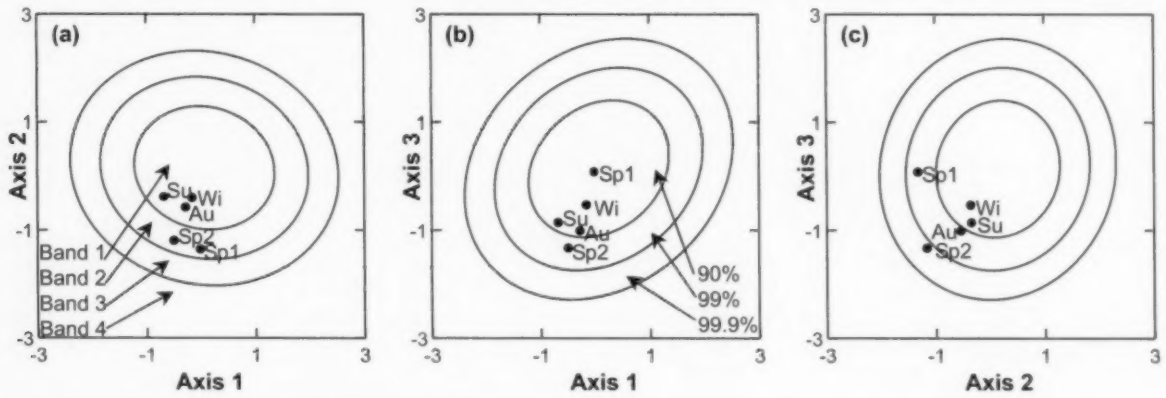
Table 3. Summary of the groups into which the exposed sites were predicted based on the autumnal sampling and where the seasons fell in the probability ellipses of the ordination space.

Streams			Genus		Family	
Location	Study site	Season	Faunal group	Band	Faunal group	Band
Continental	Mellin	Autumn 1995	5	3	4	2
		Spring 1995	5	4	4	4
		Summer 1995	5	2	4	2
		Winter 1995	5	4	4	4
		Spring 1996	5	2	4	2
Concordance with autumn			0%		50%	
Large	Fraser	Autumn 1995	4	2	2	1
		Spring 1995	4	2	2	2
		Summer 1995	4	3	2	1
		Winter 1995	4	1	2	1
		Spring 1995	4	2	2	1
Concordance with autumn			50%		75%	

Note: See Fig. 3 for a visual placement of the probability ellipse bands: Band 1, within the 90% probability ellipse; Band 2, between the 90% and 99% probability ellipses; Band 3, between the 99% and 99.9% probability ellipses; Band 4, outside of the 99.9% probability ellipse.

Fig. 3. Placement of the seasonal test samples from Spring Creek in the ordination space of reference Group 2. All three axes shown (*a–c*). The invertebrates were identified to the genus level. Sampling: Sp1, spring 1995; Su, summer 1995; Au, autumn 1995; Wi, winter 1995; Sp2, spring 1996. The 90%, 99%, and 99.9 % probability ellipses are based on the ordination scores of the reference data.



small (Hawkins and Sedell 1981; Death 1995; Zamora-Muñoz and Alba-Tercedor 1996). These changes occur as invertebrates move through their life cycles and because of short-term exclusion of taxa as a result of redistribution of invertebrates from disturbance events such as floods (Reice et al. 1990). Invertebrate assemblage structure also changed at our seasonal test sites. The magnitude and direction of the seasonal change in ordination space depended on the site, season, and the taxonomic resolution used. The seasonal change resulted in an average of 43% of the sampling dates being misclassified at the genus level and an average of 52% misclassification at the family level.

Although seasonal change was primarily a result of change in invertebrate abundance rather than composition, there was no consistency in the direction or magnitude of movement in ordination space. Therefore, there is no a priori way of knowing the influence of seasonal change on future test-site samples collected outside of autumn. There was very little difference in the sensitivity to seasonal effects between the family and genus levels.

In the future, the reference database could be expanded by the addition of multiple reference sampling dates, which would allow seasonal variation to be incorporated into the model (Furse et al. 1984; Marchant et al. 1997). Use of test samples also collected over multiple sampling dates could reduce the potential for Type I errors as a result of stochastic events or sampling errors. As an alternative, seasonal data could be applied by creating season-specific models.

Seasonal change and exposed sites

Mellin Creek was different from the reference condition based on the autumnal sampling. Cattle were using the stream as a source of water in the autumn, so they were moving through the stream and defecating in it at the time of the autumnal sampling. The impact of the cattle was detected by the reference-condition model, which was slightly more sensitive to the impact of the cattle when genus-level data were used than when family-level data were used. Autumn and other seasons fell outside of Band 1 at both taxonomic levels, probably because of a combination of stress and seasonal change.

Seasonal change of the benthic assemblage at Mellin Creek

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was also detected through the "movement of sampling dates (ordination scores) in ordination space" (data not shown). This movement resulted in some dates being similar to the reference condition, or only possibly different from it, which has implications to biomonitoring in the Fraser River catchment. A site that is disturbed could be classified as being similar to the reference condition simply as a result of seasonal variation, or if test samples were collected after a period of quiescence. Recovery of a site from a disturbance or after remediation could also be determined from the reference-condition model, but only from samples collected during the reference season.

Influence of different taxonomic levels

The taxonomic level used influenced the grouping of reference sites and the sensitivity of analysis at exposed sites. The reference groups formed by the classification are important because they are a potential source of variation and form the basis of the remaining analysis. A low number of groups results in each reference group containing a large number of reference sites and a large amount of variability. A low number of groups could result in a model that is not as sensitive to slight variations in the data as when a greater number of reference groups are formed. One model is not necessarily more correct than another, but it is important to identify how various decisions about analysis can affect the model and associated predictions. The formation of six reference groups from the genus-level data versus four formed with the family-level data set did not result in a model that was strikingly more sensitive to seasonal variation at reference sites.

Genus-level data should contain more information than family-level data. Species in a family can have different stress tolerances (Wright 1995; Zamora-Muñoz and Alba-Tercedor 1996) and life cycles (Sweeney and Vannote 1981), and the genus-level data may reflect these differences. The genus- and family-level models had similar sensitivities to the samples from the seasonal test sites (87% of the samples in Bands 1 and 2). However, at the exposed sites, the lower concordance between the seasonal and autumnal samples and the location of the seasonal samples in the probability ellipses indicated that the genus level was more sensitive than the family level to seasonal variation.

Implications of seasonal change to biomonitoring using the Fraser River catchment model

Seasonal changes of the seasonal test-site assemblages affected how the Fraser River predictive model should be used. Seasonal changes were sufficient to place some sampling dates outside of Band 1. Such placement creates uncertainty because of an inability to separate typical seasonal changes from changes caused by stress on the system. Therefore, we offer the following recommendations for use of the Fraser River reference-condition model.

First, future test-site samples should be collected in the same season as the reference samples (autumn) and should account for differences caused by invertebrate life cycles. The recovery of a site to an equivalent-to-reference condition can also be detected with test samples collected in the autumn.

Second, a gradual accumulation of seasonal data from reference sites is recommended. This strategy will allow seasonal variation to be included in the model or the creation of season-specific models in addition to autumn.

Third, caution and common sense should be used when analyzing single test samples collected in a season other than autumn. No unusual disturbance events should precede sampling, and because seasonal variation may cause a site with no apparent stresses to fall outside of the ellipses, further investigation of the site may be required.

Fourth, almost all of the seasonal variation resulted in samples falling just outside of the 90% reference ellipse. Perhaps the 99% ellipse should be used as the cutoff between equivalent-to-reference and possibly different-from-reference when genus data are used and test samples are collected outside of the autumnal season. However, this approach is not generally recommended because of a danger of Type II errors.

Finally, the most appropriate taxonomic level for future users of the Fraser catchment predictive model will depend on the level of expertise of the biologists involved. It would be more appropriate to use family level than to incorrectly identify test-site invertebrates. Identification to the family level may also be more appropriate when samples contain many early instar larvae, which are difficult to identify to lower taxonomic levels. Analysis at the family level is more appropriately used to filter out the noise associated with minor seasonal changes and stochastic events.

Acknowledgements

The authors thank T. Tuominen and Environment Canada's Fraser River Action Plan for support of this project. J. Detman, J. Kaman, R. Letchford, C. Logan, and J. Melody helped with sampling, sample processing, and invertebrate identification. A. Borkent, J. Cumming, D. Currie, and B. Kondratieff generously donated their time and effort to verify invertebrate identifications. The authors also thank J. Rosenfeld and two anonymous reviewers for their comments on the manuscript.

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Predicting mercury levels in yellow perch: use of water chemistry, trophic ecology, and spatial traits

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Abstract: Recent research suggests that wetland abundance surrounding lakes, fish trophic position, and fish community composition may influence the bioavailability of mercury (Hg) to fish. To compare the importance of these spatial and biological factors to chemical factors known to influence bioavailability, we determined the relationship between 24 lake traits and Hg concentrations in yellow perch (*Perca flavescens*; whole fish samples) for 43 northern Wisconsin lakes. Independent variables included biological traits such as fish trophic position and body condition, spatial traits such as lake hydrologic position and surrounding wetland abundance, and chemical traits such as pH and water color. The strongest predictor of fish Hg levels was pH (R^2 = 0.42; $p < 0.002$). Of the biological traits measured, yellow perch body condition explained significant additional variation (final R^2 = 0.54; p = 0.024). Trophic position explained limited variability and population abundance of planktivores and piscivores were not correlated to perch Hg levels. Regression tree models indicated that small lakes with greater than 6% wetland in their watershed have moderately elevated fish Hg levels. Our results indicate that within-lake chemistry and fish growth patterns are stronger correlates of Hg levels in yellow perch than spatial traits, trophic position, or fish community attributes.

Résumé : Des travaux récents laissent croire que l'abondance des terres humides autour d'un lac, la position trophique des poissons et la composition de la communauté ichtyenne peuvent affecter la biodisponibilité du mercure aux poissons. Afin de comparer l'importance de ces facteurs spatiaux et biologiques avec celle des facteurs chimiques connus pour leur influence sur la biodisponibilité, nous avons déterminé la relation entre 24 caractéristiques de 43 lacs du nord du Wisconsin et les concentrations de mercure chez la Perchaude (*Perca flavescens*; échantillons de poissons entiers). Les variables indépendantes incluent des caractéristiques biologiques, telles que la position trophique des poissons et leur condition physique; les variables spatiales comprennent, par exemple, la position hydrologique du lac et l'abondance des terres humides adjacentes; les variables chimiques regroupent, entre autres, le pH et la couleur de l'eau. La variable explicative la plus significative de la concentration de mercure chez les poissons est le pH (R^2 = 0,42; $p < 0,002$). Parmi les caractéristiques biologiques mesurées, la condition physique des Perchaudes explique une partie significative additionnelle de la variation (R^2 final = 0,54; p = 0,024). La position trophique n'explique que peu de la variabilité et il n'y a pas de corrélation entre l'abondance des populations de planctonophages et de piscivores et les concentrations de mercure chez les Perchaudes. Des modèles d'arbres de régression indiquent que les petits lacs qui ont plus de 6% de terres humides dans leur bassin versant ont des concentrations moyennes de mercure chez les poissons. Nos résultats montrent que les caractéristiques chimiques du lac même et les taux de croissance des poissons sont de meilleures variables explicatives des concentrations de mercure chez les Perchaudes que les caractéristiques spatiales, la position trophique ou la structure de la communauté de poissons.

[Traduit par la Rédaction]

Introduction

Atmospherically deposited mercury (Hg) bioaccumulates in freshwater food webs. Therefore, many relatively undisturbed lakes have elevated levels of Hg in fish and wildlife. Elevated Hg concentrations in planktivorous fishes can be toxic for piscivorous fishes and wildlife and hazardous for human consumption (Wiener and Spry 1996). Methyl mercury (MeHg) is the predominant form in fish tissue (Grieb et al. 1990) because it is efficiently retained in tissue and biomagnifies in aquatic food webs (Kidd et al. 1995). Previous studies on the causes of elevated fish Hg levels have established the importance of among-lake differences in limnological characteristics and morphometry. Reductions in pH (Grieb et al. 1990; Suns and Hitchin 1990; Watras et al. 1998), increases in dissolved organic matter (Driscoll et al.

Received September 21, 2000. Accepted April 6, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 14, 2001.
J15988

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 DOI: 10.1139/cjfas-58-7-1419 © 2001 NRC Canada

1995; Watras et al. 1998), and reductions in lake size (Bodaly et al. 1993) all correlate with higher fish Hg levels. However, a lake's surrounding landscape or its ecological community composition may also influence Hg bioaccumulation in fish. We examine whether ecological or landscape factors influence Hg accumulation to the same degree as limnological and morphometric characteristics.

Models of Hg bioaccumulation often incorporate trophic position under the assumption that trophic position significantly influences bioaccumulation (Cabana and Rasmussen 1994). In piscivorous fishes, increased trophic position increases Hg bioaccumulation (Cabana and Rasmussen 1994; Cabana et al. 1994; Kidd et al. 1995). However, little is known about the influence of trophic position on contaminant levels for relatively short-lived, omnivorous fishes, which may be important intermediate links for biomagnification. Relative trophic position can be measured using stable isotope analysis, in which an organism's nitrogen isotope ratio is compared to that of other organisms in a food web (Peterson and Fry 1987).

Ecological interactions may cause increased fish contaminant levels by influencing contaminant levels of food or growth rate of the fish. Few studies have examined population abundances within the fish community to determine potential impacts of predation and competition on Hg accumulation rates. In two studies, reduced population abundance caused decreases in Hg accumulation due to increased growth rate (Verta 1990) or reduced consumption of contaminated benthos (Wong et al. 1997). These results suggest that in lakes with dense fish populations, fish would exhibit reduced growth rates, causing less growth dilution and leading to higher tissue Hg concentrations. Fish body condition (a measure of weight to length ratio) has been observed to correlate negatively with Hg levels (Suns and Hitchin 1990). Body condition indicates growth efficiency (Willis et al. 1991; Fechhelm et al. 1995) and potential for growth dilution.

Spatial traits of lakes can be measured remotely using geographic information systems, and may allow natural resource managers to efficiently screen large numbers of lakes for those likely to have high fish Hg levels (Gergel et al. 1999). A lake's spatial traits include both its relative position in a watershed and the abundance of land-cover types surrounding the lake. Lake order, analogous to stream order, identifies lakes according to their hydrologic position with respect to other lakes and associated streams. Groundwater connection increases as lake order increases, causing increased alkalinity (Riera et al. 2000). Additionally, as lake order increases, catchment area increases, causing increased water color (Riera et al. 2000). Because both color and alkalinity affect fish Hg levels (Grieb et al. 1990; Watras et al. 1998), and because lake order is easy to measure, we evaluate lake order as a potential predictor of fish Hg concentrations.

Correlations between watershed attributes and aqueous Hg levels within a lake have been demonstrated through research at the landscape scale. Wetlands have been identified as significant sources of MeHg to adjacent lakes and rivers (Rudd 1995). Methyl mercury is produced and stored in wetlands (Rudd 1995), and wetland abundance correlates positively with river water MeHg concentration (Hurley et al. 1995). Additionally, wetlands are sources of dissolved organic matter, which reduces oxygen levels, thereby facilitating Hg methylation by sulfate-reducing bacteria (Gilmour et al. 1992; Crisman et al. 1998). However, little is known about the relationship between wetland abundance surrounding a lake and Hg concentrations in the lake biota (but see Driscoll et al. 1995).

In this study, we compare Hg concentrations in yellow perch (*Perca flavescens*) to the chemical, biological, and spatial attributes of 43 northern Wisconsin lakes. Our specific hypotheses are as follows: (*i*) yellow perch trophic position and planktivore population size will be positively correlated with Hg concentrations due to increased bioaccumulation and reduced growth dilution, respectively; (*ii*) yellow perch body condition will be negatively correlated to fish Hg because it will indicate fish growth efficiency; (*iii*) wetland abundance will be positively correlated to fish Hg, because wetlands are sources of MeHg; and (*iv*) lake hydrologic position will indicate Hg concentrations. Regarding hydrologic position, we expect to find the highest fish Hg levels in low alkalinity seepage lakes, intermediate Hg levels in lowland drainage lakes, which are alkaline but have elevated water color, and the lowest Hg levels in headwater drainage lakes. Hydrologic position and wetland abundance would be particularly useful predictors, because they would allow resource managers to identify lakes for potential consumption advisories using geographic information systems data.

Methods

Study site

Forty-three lakes from the Northern Highland Lake District, Wisconsin, U.S.A. were chosen for this study (46°N, 89°W). This region is characterized by 30–50 m of non-calcareous, sandy tills overlying granitic bedrock (Riera et al. 2000). Chosen lakes included all regional hydrologic types (drainage lakes, headwater lakes, and seepage lakes; Table 1). The study lakes also ranged widely in alkalinity and surrounding wetland abundance (Table 2). Five of the lakes have been routinely sampled as part of the North Temperate Lakes Long Term Ecological Research site (NTL-LTER), and one lake has been sampled as part of the Cascading Trophic Interactions Project (Bade et al. 1998).

Chemical data

Lakes were monitored for pH, alkalinity, total phosphorus, chlorophyll *a*, and color during June, July, and August of 1997–1999 (Table 2). Except as specified, all chemical data were collected and analyzed according to NTL-LTER protocols, which are available to the public for inspection at the NTL-LTER Web site (http://www.limnology.wisc.edu/catalog.html). Crampton Lake was sampled according to protocols outlined in Bade et al. (1998). Samples were collected monthly in each lake during the same season fish were collected with the exception that color data were collected in the year prior to fish collection for the NTL-LTER lakes and Crampton Lake. Total phosphorus, chlorophyll *a*, and pH were averaged over June, July, and August. Alkalinity and color were determined once, during midsummer. All parameters other than chlorophyll were collected 1 m below the lake surface, except in the five NTL-LTER lakes, where they were collected at the water surface. Color samples were filtered through 0.4-μm nucleopore filters and analyzed at 440 nm. Epilimnetic chlorophyll concentration was measured monthly to estimate primary productivity. Chlorophyll samples were collected on Fisher Type A/E glass fiber filters by raising and lowering sampling tubing at a constant rate while drawing water with a peristaltic pump. Samples were homogenized and stored in

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Table 1. Characteristics of the sampled lakes, including area, hydrologic position, fish length, Hg concentration, number of fish sampled, and whether the lake was sampled for all fish biology parameters. Lake order is placed in parentheses next to hydrologic position.

Lake name	Area (ha)	Hydrologic position[a]	Fish length (mm)		Fish Hg ($\mu g \cdot g^{-1}$)		N	Biological sampling
			Mean	SD	Mean	SD		
Allequash[b]	174	D (1)	183	9.2	0.057	0.0106	5	Y
Arrowhead	38	H (0)	153	6.6	0.025	0.0023	3	Y
Beaver	25	D (2)	164	25.8	0.084	0.0258	5	
Big	325	D (3)	145	13.2	0.036	0.0098	3	Y
Big Gibson	48	S (–2)	156	23.5	0.141	0.0384	5	
Big Muskellunge[b]	357	S (–1)	144	11.5	0.044	0.0128	4	Y
Boulder	217	D (3)	97	20.2	0.054	0.0077	5	Y
Brandy	44	D (2)	131	36.4	0.048	0.0079	9	Y
Crampton[c]	26	S (–2)	136	5.5	0.170	0.0346	3	Y
Crystal[b]	36	S (–2)	208	3.5	0.101	0.0597	3	Y
Diamond	48	S (–2)	128	36.2	0.217	0.0841	6	Y
Flora	38	H (0)	138	15.7	0.139	0.0415	3	Y
Ike Walton	569	S (–1)	159	15.6	0.140	0.0141	2	
Island	361	D (4)	134	26.5	0.055	0.0181	6	Y
Johnson	33	D (2)	156	6.1	0.053	0.0232	3	Y
Katherine	214	H (0)	211	33.2	0.080	0.0212	2	
Katinka	70	S (–2)	149	2.1	0.066	0.0164	3	Y
Lehto	32	H (0)	127	26.2	0.106	0.0629	2	
Little Crooked	61	D (2)	151	9.3	0.075	0.0141	3	Y
Little Spider	87	H (0)	155	21.3	0.040	0.0045	7	
Little Sugarbush	17	S (–2)	105	25.1	0.048	0.0104	5	Y
Little Trout	408	S (–1)	140	35.4	0.042	0.0150	4	Y
Lower Kaubeshine	79	D (1)	143	35.9	0.043	0.0144	7	Y
Lynx	121	H (0)	137	8.6	0.110	0.0100	3	Y
McCullough	90	D (2)	155	1.4	0.068	0.0057	2	
Mid	104	D (2)	163	21.2	0.066	0.0163	2	
Minocqua	809	D (2)	171	17.7	0.064	0.0142	3	
Muskesin	46	S (–2)	146	32.1	0.120	0.0410	4	Y
Nixon	49	D (2)	154	22.9	0.091	0.0201	5	
Partridge	96	H (0)	152	19	0.021	0.0097	4	
Randall	48	D (2)	152	33.2	0.068	0.0092	2	
Round	72	D (3)	111	30.5	0.067	0.0307	8	Y
Sanford	36	H (0)	133	39.8	0.130	0.0721	6	Y
Sparkling[b]	64	S (–2)	142	14.7	0.058	0.0148	3	Y
Statenaker	84	S (–2)	144	24.7	0.103	0.0172	5	Y
Stearns	96	S (–2)	126	34.3	0.037	0.0143	7	Y
Tomahawk	1495	D (2)	142	12.6	0.042	0.0025	3	
Trout[b]	1568	D (2)	161	27	0.077	0.0215	4	Y
Upper Kaubeshine	71	H (0)	135	43.8	0.045	0.0106	7	Y
White Birch	46	D (1)	151	10.6	0.053	0.0122	3	Y
White Sand	299	D (2)	135	16	0.041	0.0183	4	Y
Wild Rice	152	D (3)	120	38.3	0.068	0.0277	7	Y
Wildcat	142	H (0)	146	5.3	0.015	0.0010	3	Y

Note: SD, standard deviation.
[a]S = seepage; H = headwater; D = drainage; lake order in parentheses.
[b]NTL-LTER lake.
[c]Cascading Trophic Interactions lake.

methanol for 24 h prior to spectrophotometric determination of chlorophyll concentration. For the NTL-LTER lakes, chlorophyll data were taken from Sanderson (1998).

Biological data

Biological traits measured included yellow perch body condition, age, total length, length at ages 1–3, total Hg concentration, stable nitrogen isotope ($\delta^{15}N$) signature, and population density, total density of other planktivorous fishes, and predator density (Table 2). Fish sampling was conducted between June and August in 1998 and 1999. Crampton Lake was sampled in 1997 and 1999. Yellow perch were collected by a combination of angling, beach seines, vertical gill nets, fyke nets, and electrofishing.

To evaluate the impact of planktivore and piscivore density, 30 of the lakes were sampled to estimate relative abundances of major feeding guilds. In these lakes, three fyke nets were set in the litto-

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Table 2. Descriptive statistics of selected variables measured in the study lakes during the summers of 1997–1999. Transformation column indicates the transformation that was used to achieve normality prior to linear regression analysis.

Attribute	No. lakes	Minimum	Maximum	Mean	SD	Transformation
Limnology						
Alkalinity ($meq \cdot L^{-1}$)	43	7	1 859	569	395	Square root
Phosphorus ($\mu g \cdot L^{-1}$)	43	2.3	30.0	13.2	7.1	Square root
Chlorophyll ($\mu g \cdot L^{-1}$)	43	1.4	35.5	7.0	6.2	Log
Water color (440 nm)	43	0.22	6.02	1.45	1.19	Log
pH	43	5.6	9.1	7.7	0.8	None
Fish biology						
Yellow perch abundance	30	6	1 385	244	327	Log
Other planktivore abundance	30	5	1 288	288	346	Log
Piscivore abundance	30	3	518	92	104	Log
Perch body condition	30	–0.19	0.17	0.00	0.08	None
Perch Hg concentration ($\mu g \cdot g^{-1}$)	43	0.02	0.22	0.07	0.04	Log
Perch corrected $\delta^{15}N$	43	1.3	8.1	4.7	1.9	None
Perch length (mm)	43	97	211	146	22	None
Length at age 1 (mm)	30	48	86	63	10	Log
Perch age (years)	30	1[a]	7[a]	3	1.0	Square root
Spatial						
Lake order	43	–2	4	0.5	1.8	None
Total watershed area (ha)	42	66	2 541	539	571	Log
Percent wetlands	43	0	76	17	17	Arcsin(square root)
Maximum depth (m)	43	2	36	12	7.6	Square root
Lake area (ha)	43	17	1 568	204	337	$(Log)^{-1}$
SDF[b]	43	1.04	4.21	1.88	0.66	Log
Perimeter (m)	43	1327	49 927	8665	9826	$(Log)^{-1}$

Note: SD, standard deviation.
[a]Youngest and oldest fish; averages across lakes were 1.3 and 5.7 years, respectively.
[b]SDF = shoreline development factor = length / $[2(\pi \cdot \text{area})^{0.5}]$.

ral zone and a vertical gill net with five mesh sizes (19-, 32-, 51-, 64-, and 89-mm stretch mesh) was set in the pelagic zone for one diel cycle. Additionally, two 30-min electrofishing transects were performed. We grouped fishes as planktivores or piscivores based on general feeding habits described in Becker (1983). Piscivorous fish species included burbot (*Lota lota*), lake trout (*Salvelinus namaycush*), northern pike (*Esox lucius*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieui*), walleye (*Stizostedion vitreum*), and muskellunge (*Esox masquinongy*). Planktivores included pumpkinseed (*Lepomis gibbosus*), rock bass (*Ambloplites rupestris*), warmouth (*Lepomis gulosus*), black crappie (*Pomoxis nigromaculatus*), and bluegill (*Lepomis macrochirus*).

Yellow perch relative body condition was based on residuals from a linear regression of log-transformed total length and body mass (n = 1487) (Fechhelm et al. 1995). Fish under 75 mm were eliminated from the analysis owing to the difficulty of measuring their mass in the field. Twenty-seven extreme outliers were removed using a studentized residual test. The remaining 1460 residuals were averaged by lake to calculate each lake's relative body condition. Yellow perch age and length at ages 1–3 were determined by reading at least five scales collected posterior to the pectoral fin, assuming a constant size ratio of body length to scale diameter.

We determined the tissue Hg wet weight concentration of 183 fish from the 43 study lakes. The number of fish sampled per lake ranged between 2 and 9, with at least three fish sampled for 38 of the lakes. When possible, fish chosen for analysis were approximately 150 mm in length, to reduce variability in Hg concentrations caused by variability in fish length (Table 1). Whole fish were ground and acid digested and total Hg concentration was determined using flow-injection, cold vapor atomic absorption spectroscopy at the Wisconsin State Lab of Hygiene (Sullivan and Delfino 1982). The limit of detection is 4 $ng \cdot g^{-1}$ and the limit of quantification is 10 $ng \cdot g^{-1}$. Quality control included analytical and procedural blanks, calibration standards, a standard reference material (lobster hepatopancreas, National Research Council of Canada), and recovery of spiked samples. Differences between replicates averaged 7% (n = 21, standard deviation, SD = 7%) and recovery of spikes averaged 95% (n = 22, SD = 8%). For 14 of the fish, ranging in whole body concentration from 0.03–0.25 $\mu g \cdot g^{-1}$, a muscle sample was also analyzed to enable determination of the muscle to body concentration ratio.

As a potential predictor of fish Hg levels, we calculated yellow perch relative trophic position using stable isotope analysis. Trophic position was estimated for each lake as average perch $\delta^{15}N$ minus Cladocera $\delta^{15}N$ ($\delta^{15}N = [(R_{sample}/R_{standard}) - 1]1000$, where $R = {}^{15}N/{}^{14}N$; Peterson and Fry 1987). While $\delta^{15}N$ may vary among lakes for several reasons (Gu et al. 1996), the difference between perch and Cladocera within a lake should be proportional to the trophic position of perch relative to herbivores (Cabana and Rasmussen 1996). Cladocera were collected for stable isotope analysis using replicate water column tows of a 150-µm mesh Wisconsin net. From each lake several hundred individual herbivorous Cladocera were sorted, pooled, and dried for stable isotope analysis. Ground whole body fish samples were dried at 65°C and analyzed for $\delta^{15}N$. Samples were analyzed using a Micromass NC2500 continuous-flow mass spectrometer (U.S. Environmental Protection Agency, Mid-Continent Ecology Division, Duluth, Minn.) and a Finnigan Delta+ infrared mass spectrometer (Water Research Center, University of Alaska, Fairbanks, Alaska). Seven paired samples indicated no significant difference between machines.

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Table 3. Pearson product–moment correlation between yellow perch Hg and selected lake attributes.

Attribute	No. lakes	Correlation coefficient
Alkalinity	43	–0.65
pH	43	–0.65
Body condition	30	–0.59
Corrected $\delta^{15}N$	43	0.38
Lake order	43	–0.26
Water color	43	0.25
Length at age 1	30	0.23
Length at age 2	30	–0.23
Length at age 3	28	–0.11
Length	43	0.07
Age	30	0.02

Spatial data

Spatial data included lake morphometry, watershed area, lake order, and surrounding wetland abundance (Table 2). Data on lake area, perimeter, maximum depth, and watershed area were obtained with ArcView using methods and sources described in Gergel et al. (1999). We define watershed area as the direct drainage watershed. In drainage lakes, the watershed boundary extended up to the outlet of the immediate upstream lake. Total watershed area, terrestrial watershed area, and total watershed to lake area ratio were all examined. Lake order was determined using a modification of the method of Riera et al. (2000). Lake order is a numerical surrogate for groundwater influx and hydrologic position along a drainage network, with the highest number indicating the lake lowest in a watershed. We define lake order as follows: –2 indicates isolated seepage lakes, –1 indicates seepage lakes connected by intermittent streams, 0 indicates headwater drainage lakes, and 1 through 4 indicate drainage lakes, with the number indicating the order of the stream that exits the lake (Riera et al. 2000). Wetland proportion was determined for a zone 500 m distant from the lakeshore that fell within the drainage area. Wetlands were defined using the methods of Gergel et al. (1999) and included terrestrial wetlands, emergent macrophytes, and floating macrophytes. Wetland proportion data were arcsin(square root) transformed.

Statistical analyses

Data were categorized as chemistry, fish biology, or spatial traits (Table 2) and models were built using each separate category and all categories in combination. Regression trees and linear regression were both used to determine the best fitting models. Regression trees are a binary partitioning approach whereby a data set is progressively split into subsets that most significantly reduce the variability of the response variable (Clark and Pregibon 1992). We did not transform predictor variables because regression tree results are invariant to predictor variable transformation (Clark and Pregibon 1992). For each group of potential predictor variables, we built trees in which the minimum number of lakes per node was five and the minimum proportionate reduction of error (PRE) per split was 0.01. Of the resulting tree, we determined optimal tree size by cross-validation and tree pruning (Clark and Pregibon 1992; Lamon and Stow 1999). Specifically, for each potential tree, at each potential tree size, the data set was split into 10 subsets, a separate tree was built in the absence of each subset, and the accuracy with which the tree predicted each subset was determined. Cross-validation was repeated by bootstrapping 1000 times and the tree size with the lowest average variance was selected. In instances where the difference was ambiguous between tree sizes, we used a combination of box plot inspections and biological interpretation to determine optimum tree size. Residual plots of final trees were examined for homoscedasticity and normality. For final tree results, we report PRE as an indicator of the total amount of variability that a specific tree explained.

Forward selection stepwise linear regression was performed following Draper and Smith (1998). We built models using all potential predictor variables and a subset of predictor variables chosen based on Pearson product–moment correlations and visual inspection. Addition and removal of variables were conducted manually based on p values, biological interpretation, and examination of plots. Unless otherwise noted, the cutoff point for predictor variable addition was $p < 0.05$; evaluations at higher cutoff levels ($p < 0.10$) did not change the final results observed. We used standard residual plots to examine final models for homoscedasticity and normality, and when necessary, transformed predictor variables (Table 2). For all models, Hg concentration was log transformed and then averaged by lake, unless otherwise specified. All correlation coefficient (r) values reported in the text are Pearson product–moment correlation coefficients.

Results

Within- versus among-lake variability

The tissue Hg concentration of the 183 sampled fish ranged from 0.01–0.31 $\mu g \cdot g^{-1}$ (Table 1). The mean concentration by lake was 0.075 $\mu g \cdot g^{-1}$, the standard deviation averaged 0.021, and the standard error averaged 0.011. Analysis of covariance using lake as a categorical predictor and fish length as a covariate indicated that the majority of variability in fish Hg levels was explained by interlake variations ($R^2 = 0.78$; $p < 0.0001$). Fish length explained a significant but very small proportion of variance ($R^2 = 0.04$; $p < 0.0001$). The effects of among-lake variation (MS = 1.23; 42 df) and fish length (MS = 2.91; 1 df) were greater than unexplained variance (MS = 0.08; 139 df). Regression analysis of the ratio of muscle (M) to whole body (B) Hg concentration produced a relationship of $B = 0.004 + 0.64M$ ($R^2 = 0.995$; $p < 0.0001$; $n = 14$).

Fish Hg was most strongly correlated with alkalinity and pH. Mercury concentration was negatively correlated with body condition and positively related to corrected $\delta^{15}N$. Correlation with age, total length, and length at ages 1–3 (indices of growth rate) were relatively weak (Table 3).

Regression tree analysis

Regression trees were built using exclusively chemical, biological, or spatial data. Of the three types of data, trees based on biological data explained the most variability in fish Hg levels, with a total proportionate reduction of error (PRE) of 0.64. Trees based on limnological data explained a similar amount of variability (PRE = 0.56) and spatial trees explained the least variability (PRE = 0.33).

The biological tree displayed highest Hg levels for fish with low relative body condition and lowest Hg levels for fish with high body condition and low $\delta^{15}N$ signature (Fig. 1). The limnological tree indicated that Hg levels were highest in lakes of pH less than 6.7 (Fig. 2). The spatial tree indicated that small lakes (area < 63.9 ha) with abundant wetlands (abundance > 5.7%) had elevated Hg levels (Fig. 3). Among the three separate regression trees, the most significant single predictors observed were pH, which reduced er-

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Fig. 1. Final tree results for biological predictors of fish Hg levels. Mean Hg levels are reported (μg·g^{-1} wet weight), with the higher levels in right-hand branches. PRE, proportionate reduction of error; condition, yellow perch body condition; δ^{15}N, perch corrected nitrogen isotope signature.

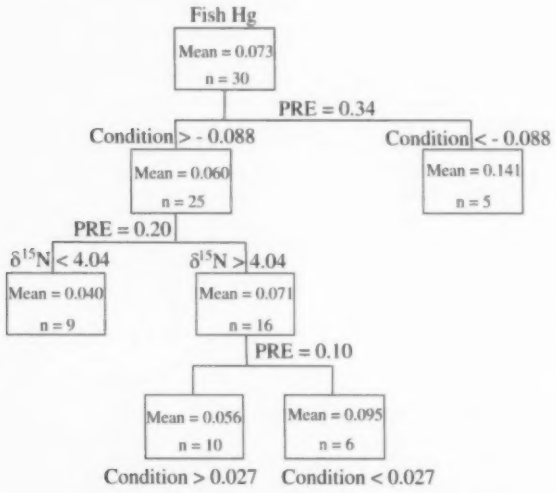


Fig. 2. Final tree results for chemical predictors of fish Hg levels. Mean Hg levels are reported (μg·g^{-1} wet weight), with the higher levels in right-hand branches. PRE, proportionate reduction of error; P, epilimnetic phosphorus (μg·L^{-1}).

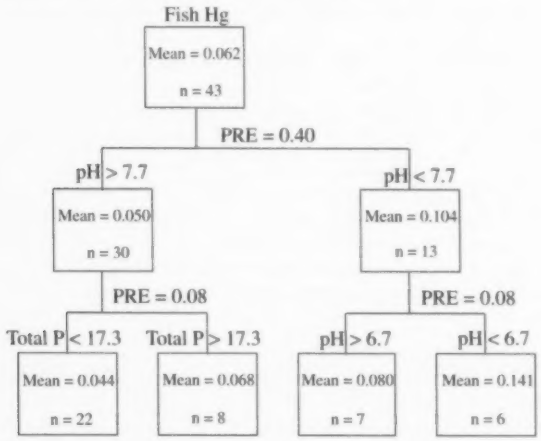


Fig. 3. Final tree results for spatial predictors of fish Hg levels. Mean Hg levels are reported (μg·g^{-1} wet weight), with the higher levels in right-hand branches. PRE, proportionate reduction of error; area, lake area (ha).

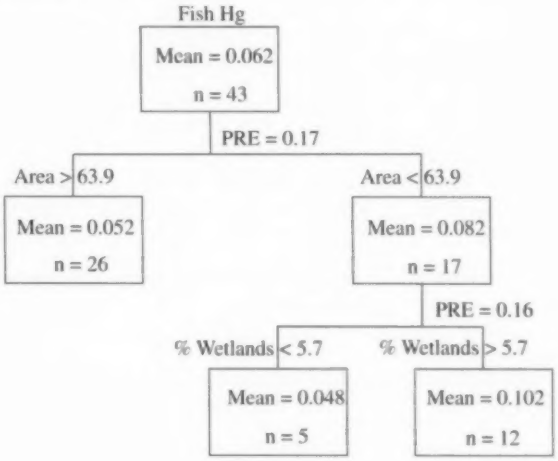
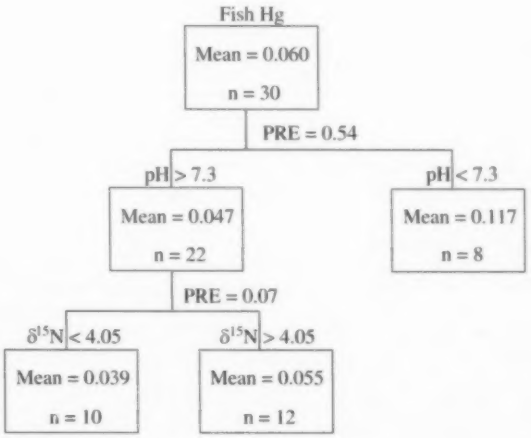


Fig. 4. Final tree results of tree combining the best predictors generated in separate models. Mean Hg levels are reported (μg·g^{-1} wet weight), with the higher levels in right-hand branches. PRE, proportionate reduction of error; δ^{15}N, perch corrected nitrogen isotope signature.



ror by 0.48 over two splits, and fish body condition, which reduced error by 0.44 over two splits.

To evaluate the relative importance of limnological, biological, and spatial predictors in the same model, we built a tree using the predictors retained in the separate tree models: pH, phosphorus, fish body condition, fish δ^{15}N, lake area, and percent wetland abundance (Fig. 4). In this tree, the majority of variability was explained by pH, with a PRE of 0.54. Among the lakes with pH greater than 7.3, the lowest perch Hg concentrations were found in lakes where corrected perch δ^{15}N was less than 4.05. This split improved the PRE by 0.07, producing a final model that explained 0.61 of the total variance.

Linear regression analysis

For stepwise regression, we chose six predictor variables that had relatively high correlation coefficients with Hg (Table 3): two limnological traits (pH and water color), two biological traits (body condition and corrected δ^{15}N), and two spatial traits (lake order and lake area). Additionally, we built a forward selection model including all potential predictors (Table 2). Both models selected pH and fish body

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Fig. 5. The relationship between lake pH and yellow perch Hg concentration (n = 43; r = –0.65). Note log y-axis.

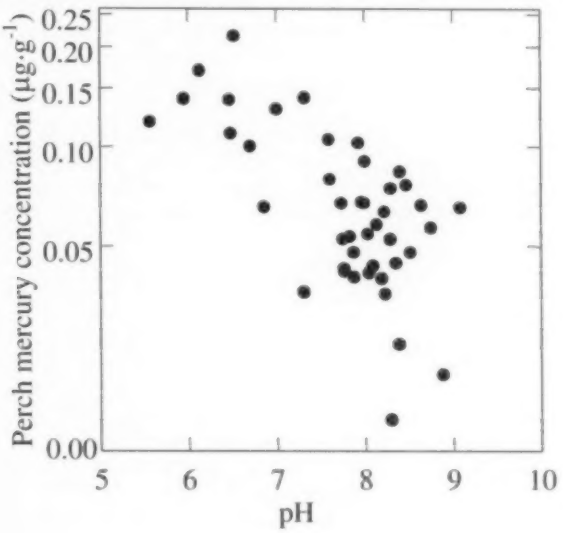
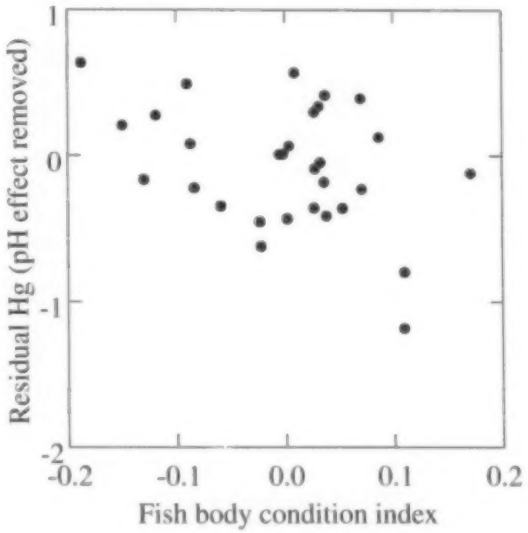


Fig. 6. The relationship between yellow perch relative body condition and the residual error from the pH vs. Hg regression (n = 30; r = –0.38).



condition in the final model. As in the limnological and mixed predictor regression tree models, pH explained the most variability in fish Hg levels (R^2 = 0.42; p = 0.0018). Fish body condition explained significant additional variability, as indicated by a partial F test (F = 5.74; p = 0.024) and also a linear regression of the residuals of the pH versus Hg regression (p = 0.037; R^2 = 0.15; Fig. 6). The combined model (log(Hg) = –0.188 – 0.343pH – 2.39condition; R^2 = 0.54) indicated that both predictors were negatively correlated with yellow perch Hg levels (Figs. 5 and 6). No predictors added significantly to the variability explained by the pH and body condition model.

Biological patterns

Regression analyses indicated that neither abundance of yellow perch (p = 0.77), planktivores (p = 0.55), nor piscivores (p = 0.1) was significantly correlated with perch Hg. However yellow perch abundance was significantly correlated with epilimnetic phosphorus (R^2 = 0.27; p = 0.003). Body condition of yellow perch, the strongest biological predictor of Hg levels in both the biological tree model and the combined multiple regression model, was also negatively correlated with pH. The correlation between condition and pH (r = –0.46) makes it difficult to confirm a significant body condition effect on Hg independent of pH. To determine whether body condition is correlated with fish Hg levels for individual fish within lakes, we performed an analysis of covariance (ANCOVA) using lakes as covariates and individual fish body condition as the predictor variable. For the 128 fish taken from the 30 lakes analyzed for biological data (Table 1), we determined that body condition was significantly related to Hg levels ($F_{1,128}$ = 4.113; p = 0.045), independently of the lake effect. Because fish in a given lake experience the same pH, we infer that body condition is related to Hg independently of pH.

Spatial patterns

Initial examination of scatterplots and correlation coefficients did not identify any spatial lake attributes as significantly related to fish Hg levels. However, based on previous research, and the results of the regression tree, we expected some influence of surrounding wetland abundance on Hg patterns. Therefore, we further examined subsets of the data to identify the circumstances in which wetland abundance was correlated to fish Hg levels. When only circumneutral lakes (7 < pH < 8.8) were examined, there was a significant but weak positive relationship (p = 0.029; R^2 = 0.15; n = 31). When lakes were further constrained by deletion of seepage lakes, this strengthened the positive association between wetland abundance and perch Hg levels (p = 0.001; R^2 = 0.39; n = 25) (Fig. 7). Thus the strongest correlation between wetland abundance and fish Hg levels was found for circumneutral drainage lakes. Lake order was not significantly related to mean Hg levels (one-way analysis of variance, ANOVA; p = 0.46; 6 df), nor was watershed area (linear regression analysis using total watershed area; p = 0.20; 40 df). However, hydrologic position did affect the variability among lakes. The coefficient of variation (CV) of fish Hg concentration was higher in seepage (CV = 0.57; n = 13) and headwater (CV = 0.66; n = 10) lakes than in drainage lakes (CV = 0.25; n = 20) (Fig. 8).

Discussion

Our findings indicate that: (*i*) lake pH explained the majority of variability in Hg concentrations; (*ii*) fish-specific biological traits (body condition or $\delta^{15}N$) explained additional variability beyond that explained by pH; and (*iii*) watershed attributes, such as percent wetland abundance, did not correlate strongly with Hg concentrations, and were generally

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Fig. 7. The relationship between perch Hg concentration and proportion wetlands when drainage lakes of circumneutral pH are considered (n = 25; r = 0.63).

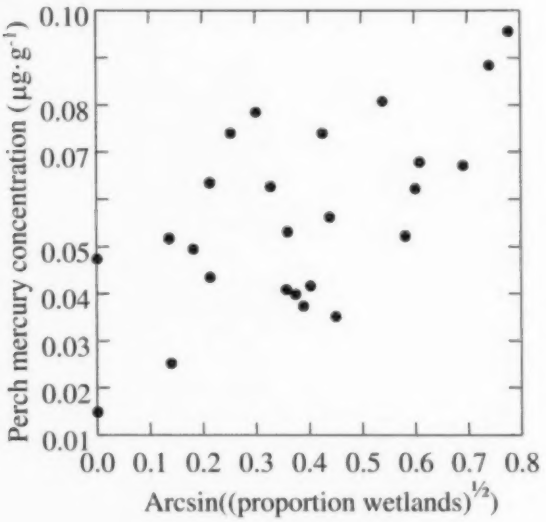
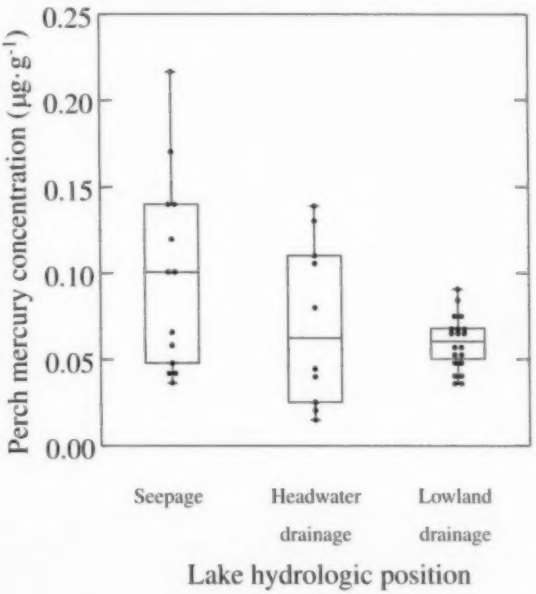


Fig. 8. The relationship between lake hydrologic position and yellow perch Hg concentration. Seepage lakes have lake orders of –2 and –1, headwater drainage lakes have lake order of 0, and lowland drainage lakes have lake orders between 1 and 4. Refer to Methods for additional description of lake order.



only relevant for subsets of the lakes. Although biological traits were significant in most models, surprisingly little variability was explained by trophic position (as estimated by $\delta^{15}N$) or community interactions (abundance of piscivores or planktivores).

When lakes were examined using a combination of all predictor types, pH explained the most variability. This finding corroborates earlier studies demonstrating the correlation between pH and Hg bioaccumulation (e.g., Grieb et al. 1990; Suns and Hitchin 1990; Watras et al. 1998). In fact, the correlation between pH and fish Hg in our study (r = –0.65) is virtually identical to that for yellow perch found by Grieb et al. (1990) (r = –0.63). Studies on the mechanism of this relationship indicate that more acidic lakes have higher aqueous MeHg concentrations, leading to higher availability at the base of the food web (Xun et al. 1987; Watras et al. 1998). Additionally, acidification may stimulate sediment MeHg production by sulfate-reducing bacteria (Gilmour et al. 1992).

Biological predictors

Other studies have demonstrated the potential importance of both diet shift (Snodgrass et al. 2000) and zooplankton food web complexity (Stemberger and Chen 1998) for MeHg bioaccumulation in omnivores. However, we found no evidence that trophic position impacted yellow perch Hg levels to the same extent as pH did. The tree models and correlation coefficients indicated that $\delta^{15}N$ was correlated with Hg concentration in yellow perch but did not explain much of the variation in Hg levels. Yellow perch are opportunistic omnivores that forage on zooplankton, benthic invertebrates, and small fishes as a function of perch size and prey availability (Becker 1983). However, yellow perch exhibit several life history attributes that may weaken the impact of trophic position on Hg levels. These include a relatively short life span, which reduces the potential for biomagnification from food-borne sources (de Freitas et al. 1974), and diet variability between pelagic and benthic sources, which may cause inconsistency in prey Hg concentrations (Cabana et al. 1994). Our results contrast with the high impact of trophic position for Hg levels in large, long-lived piscivores (Cabana et al. 1994; Kidd et al. 1995). For omnivorous yellow perch evaluated within a single region, among-lake chemical variation is much more influential on contaminant levels than dietary variation. Therefore, models of Hg accumulation based on trophic position (e.g., Cabana and Rasmussen 1994) may not be appropriate for species such as yellow perch.

Contrary to our expectations, we observed no effect of abundance of yellow perch, other planktivores, or piscivores on the concentration of Hg in yellow perch. Competition and predation have been demonstrated to impact fish Hg concentrations in a manipulated lake (Verta 1990) and increased benthivorous fish abundance has been shown to increase Hg transfer rates from benthic invertebrates to fishes (Wong et al. 1997). Nevertheless, the lack of significant relationships between our fish abundance estimates and yellow perch Hg concentrations may indicate that these mechanisms have little impact on many natural systems. In our data set, the lack of significant relationship between yellow perch abundance and Hg concentrations may result from the positive correlation between abundance and phosphorus concentration. If the increased abundances are facilitated by higher nutrient availability, then they may not indicate competition or individual growth rate.

Some comparative studies have standardized for fish size by developing a size-to-Hg regression for each lake (e.g., Bodaly et al. 1993). However, among-lake variation in fish

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size explained little variability in Hg levels for the yellow perch in our study and the study by Watras et al. (1998). In our ANCOVA using a lake effect and a fish length effect, among-lake differences explained the majority of variation in Hg, indicating that for yellow perch in the size range caught during our study, fish size was relatively unimportant.

Body condition indicates fish nutritional status at a given age (Fechhelm et al. 1995) and may influence Hg bioaccumulation rate. Among the biological predictors we evaluated, fish body condition displayed the strongest correlation with Hg concentrations. Although fish body condition has received little attention in bioaccumulation literature, Suns and Hitchin (1990) demonstrate a negative relationship between fish Hg and body condition among 16 lakes. However, lake acidity impacts body condition (Mills et al. 2000). Because of limited sample size, Suns and Hitchin (1990) were unable to distinguish a relationship between body condition and Hg beyond the impact of pH.

In our study, lower pH lakes had fish with lower body condition. However, two lines of evidence in our study indicated that fish with lower body condition had higher Hg concentrations, and that this relationship was independent of pH. First of all, analysis of residuals demonstrated that once the correlation between Hg and pH was removed, Hg was still negatively correlated with body condition. Additionally, ANCOVA with a lake effect and a body condition effect showed a significant relationship between body condition and fish Hg, even after the effects of all among-lake variations (including pH) were removed.

Based on our results, we hypothesize that body condition indicates fish growth patterns that cause elevated Hg concentrations. Fast growing fishes exhibit "growth dilution"; they reach a given size more efficiently, have spent proportionately less energy consuming and respiring to reach that size, and therefore have lower tissue contaminant concentrations per unit mass (de Freitas et al. 1974; Norstrom et al. 1976). Body condition is correlated with growth rate (Willis et al. 1991) but body condition is more indicative of current environmental constraints on growth than measures of past growth. For example, growth in individual years can be variable due to fluctuations in population densities (Fechhelm et al. 1995) but scale-derived age only estimates growth rate of prior years. Because body condition changes rapidly in response to environmental perturbation (e.g., Mills et al. 2000), it will be sensitive to conditions that change growth dilution. Finally, body condition is much easier to estimate than growth rate, requiring only length and mass data. Future research could evaluate the use of body condition guidelines for fish consumption advisories.

The fact that more acidic lakes may contain fish with lower body condition has been observed in previous studies (Suns and Hitchin 1990; Mills et al. 2000), but its implications for Hg bioaccumulation merit further consideration. More acidic lakes may have fish with lower body condition because of reduced availability of preferred food items (Mills et al. 2000) or the physiological stress associated with ion balance maintenance (Dennis and Bulger 1995). We know of no examinations of whether reduced growth efficiency (as indicated by body condition) is part of the mechanism by which acidic lakes have higher Hg bioaccumulation in fish. Watras et al. (1998) observed a steeper and more significant relationship between pH and fish Hg than between pH and Hg of lower trophic levels (crustacean zooplankton or planktonic seston), suggesting that Hg biomagnification in fish (as compared to lower trophic levels) is more significant in low pH lakes. Future studies could explicitly evaluate the relationship between pH, body condition, and biomagnification to determine whether increased biomagnification is an additional mechanism for higher fish Hg concentrations in low pH lakes.

Spatial predictors

Although we selected lakes that ranged widely in lake order and wetland abundance, neither trait was strongly related to fish Hg levels. Our data did not support the hypothesis that higher fish Hg levels would occur in seepage and lowland drainage lakes. We attribute the increased variation of fish Hg concentrations among seepage lakes to the fact that those lakes have the greatest among-lake variability in pH. The variability in pH among seepage lakes results from weak connections to underlying groundwater, which reduces alkalinity (Riera et al. 2000 and references therein). The lack of increase for lowland lakes indicates that for this region, correlates of lake order such as catchment size and water color are relatively unimportant.

The spatial tree model indicated that smaller lakes have higher fish Hg levels, which is consistent with the work of Bodaly et al. (1993). They attribute the negative correlation between lake size and fish Hg to higher water temperatures in smaller lakes causing increased methylation. Observations of increased methylation in warm littoral sediments (Ramlal et al. 1993) indicate that smaller lakes have higher biota Hg levels due to increased within-lake methylation. However, reduction of lake size may also increase the effect of allochthonous inputs of organic matter by increasing the proportionate influx of wetland-derived materials compared to the total lake volume.

Despite evidence that wetlands are sources of MeHg, in this study they only exerted quantitative impacts on fish Hg levels when (*i*) within-lake chemistry was controlled for by examining only circumneutral lakes or (*ii*) there was a relatively strong potential for watershed loading into the lake (i.e., drainage lakes or small lakes). In regression tree models, wetland abundance only correlated with elevated Hg levels in small lakes, suggesting that reduction in lake size increases the potential for input of wetland-derived MeHg or methylation substrate (i.e., dissolved organic carbon, DOC), rather than simply increasing within-lake methylation rates. In our linear regression models, the observation that perch Hg and wetland abundance were only correlated in drainage lakes supports the general conclusion that lake–wetland interactions are stronger and more easily predicted for drainage lakes. This is consistent with Gergel et al. (1999), who observe that lowland lakes have stronger lake–wetland interactions in wetland input of allochthonous DOC, which may increase Hg methylation (Gilmour et al. 1992; Crisman et al. 1998) and reduce photodegradation rates (Sellers et al. 1996). When we constrained pH in the linear regression model of wetland abundance versus fish Hg, the correlation strengthened. Previous research demonstrates that pH affects Hg methylation and consequent bioavailability to fish (Xun

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et al. 1987; Watras et al. 1998), and our results indicate that this within-lake Hg speciation overshadows the effect of MeHg loading from adjacent wetlands.

Although our data range widely in wetland abundance, the range in concentrations of DOC is generally lower than the range found in other studies (Driscoll et al. 1995; Gergel et al. 1995; Watras et al. 1998). As DOC has been linked to wetland loading of MeHg into lakes (Driscoll et al. 1995), the relatively weak impact of wetland abundance we observed may be partially attributable to the relatively low range in DOC.

In our study, variability among lakes in hydrologic position, surrounding habitat features, and fish community traits did not strongly influence Hg levels in yellow perch. Given our initial objective of predicting biota Hg levels using remotely sensed data, it is unfortunate that in northern Wisconsin lakes, we can best predict Hg levels in those systems lacking conditions conducive to high Hg bioaccumulation (i.e., only in alkaline systems). However, spatial features could be used to identify lakes likely to have high fish contaminant levels. For example, based on our regression tree models, lakes smaller than 64 ha and having greater than 6% wetlands within a catchment buffer strip would be the lakes most likely to have high biota Hg levels. Also, if data on pH or a correlate (e.g., alkalinity or conductivity) were readily available, they could be used in combination with hydrologic position (seepage versus drainage) and wetland abundance to identify the lakes likely to have the highest contaminant levels. In regions containing thousands of lakes, such as the Great Lakes states and provinces of the U.S.A. and Canada, such approaches may be useful to identify high-risk lakes.

Acknowledgements

We thank S.B. Baines, E.M. Bennett, J. Brunswick, L.B. Cleckner, J.J. Cole, G.S. Cumming, T.E. Essington, S.E. Gergel, P.R. Gorski, J.P. Hurley, T. Jaecks, K. Kapcuzinski, S. Kloehn, T.K. Kratz, E.C. Lamon, N. Lueck, D.B. Lewis, M.L. Pace, J.L. Riera, J.M. Schell, D. Stelzer, J. Thoyre, C.J. Watras, K.E. Webster, J.G. Wiener, J. Wight, K.A. Wilson, M. Wise, R. Wolchko, A.C. Yannarell, and the Trophic Cascade Project for helpful discussions, reviews of the drafts, unpublished data, and (or) help in the field or lab. Thanks are also due to N. Haubenstock and T. Howe at the Stable Isotope Laboratory, University of Alaska, Fairbanks, and R. Schultz and G. Bowman at the Wisconsin State Laboratory of Hygiene. The constructive feedback of two anonymous reviewers was greatly appreciated. Project financial assistance was provided by the N.S.F. LTER and IGERT programs, the Andrew W. Melon foundation, and an Anna Grant Birge grant. B. K. Greenfield was supported on a U.S. EPA STAR Fellowship.

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Impact of zebra mussels (*Dreissena polymorpha*) on the pelagic lower trophic levels of Oneida Lake, New York

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Abstract: We analyzed a data series on nutrients, phytoplankton, zooplankton, and young-of-the-year fish from Oneida Lake, New York, to test several hypotheses relating the response of the pelagic food web to grazing by zebra mussels (*Dreissena polymorpha*). System-wide grazing rates increased by one to two orders of magnitude after zebra mussel introduction. The most dramatic change associated with dreissenid grazing was increased water clarity and overall decrease in algal biovolume and Chl *a*. Contrary to predictions, primary production did not decline. We attribute the lack of whole water column decline in primary productivity to the compensating effect of increased water clarity resulting in deeper penetration of photosynthetically active radiation. We observed no change in total or dissolved phosphorus concentrations. Although algal standing crop declined, *Daphnia* spp. biomass and production did not, but dominance shifted from *Daphnia galeata mendotae* to *Daphnia pulicaria*. Consistent with our findings in the lower food web, we found no evidence that zebra mussels had a negative impact on young yellow perch (*Perca flavescens*) growth, biomass, or production. Thus, despite the order of magnitude increase in grazing rates and associated decrease in algal biomass, pelagic production at primary, secondary, and tertiary levels did not decline in association with zebra mussels.

Résumé : Nous avons analysé des séries de données sur les nutriments, le phytoplancton, le zooplancton et les poissons de l'année au lac Oneida, New York, afin de vérifier plusieurs hypothèses relatives aux effets du broutage par les Moules zébrées (*Dreissenia polymorpha*) sur la chaîne alimentaire pélagique. À l'échelle du système, les taux de broutage ont augmenté d'un facteur de 10 à 100 après l'introduction des Moules zébrées. Le changement le plus spectaculaire amené par le broutage des moules a été une augmentation de la limpidité de l'eau et un déclin du biovolume général des algues et de la concentration de Chl *a*. Cependant, contrairement à nos attentes, la production primaire n'a pas baissé. Nous attribuons ce maintien de la production primaire dans toute la colonne d'eau à l'effet compensatoire de la limpidité accrue de l'eau qui a permis à la radiation impliquée dans la photosynthèse de pénétrer plus en profondeur. Il n'y a pas eu de changement dans les concentrations du phosphore total, ni du phosphore dissous. Bien que la biomasse des algues ait diminué, la biomasse des *Daphnia* spp. et leur production se sont maintenues; *Daphnia pulicaria* a cependant remplacé *Daphnia galeata mendotae* comme espèce dominante. Il n'y a aucune indication que les Moules zébrées ont un effet négatif sur la croissance, la biomasse ou la production de la Perchaude (*Perca flavescens*), ce qui est conforme à nos observations sur les maillons inférieurs du réseau alimentaire. Ainsi, malgré un accroissement d'environ 10 fois des taux de broutage et le déclin qui en a résulté dans la biomasse des algues, la production pélagique aux niveaux primaire, secondaire et tertiaire n'a pas diminué en présence des Moules zébrées.

[Traduit par la Rédaction]

Introduction

The most prevalent perturbation to aquatic ecosystems that is mediated through anthropogenic vectors is the introduction of exotic species (e.g., Mills et al. 1994). To date, 146 nonindigenous species have been recorded as established in the Laurentian Great Lakes alone (Mills et al. 1994), and many studies have focused on the impact of these exotics on associated ecosystems (e.g., Strayer et al. 1999). In particular, the recent invasion of the zebra mussel (*Dreissena polymorpha*) in North American freshwater lakes and rivers has caused concern because of their high filtration capacity and their ability to alter food web structure (e.g., Padilla et al. 1996; Caraco et al. 1997).

Received April 18, 2000. Accepted November 2, 2000. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 15, 2001.
J15730

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 DOI: 10.1139/cjfas-58-7-1430 © 2001 NRC Canada

In this study, we analyzed a data series on nutrients, phytoplankton, zooplankton, and young-of-the-year (YOY) yellow perch (*Perca flavescens*) from Oneida Lake, New York, to test several hypotheses relating the response of a food web to grazing by zebra mussels. The importance of these processes will vary seasonally. Specifically, we hypothesized that (*i*) total phosphorus (TP) will not decrease but will be partitioned into more soluble reactive phosphorus (SRP) and less total particulate phosphorus (TPP) due to the lower algal biomass in the water column (Heath et al. 1995; Mellina et al. 1995; Caraco et al. 1997); other dissolved nutrients (nitrate, silica) will be less affected because phosphorus is the limiting nutrient (Johengen et al. 1995); (*ii*) phytoplankton biomass (as chlorophyll *a* (Chl *a*)) will decrease, leading to a decrease in primary productivity and an increase in water clarity (Holland 1993; Fahnenstiel et al. 1995; Caraco et al. 1997), and phytoplankton community composition will shift to grazer-resistant forms, such as large cyanobacteria or large diatoms (Smith et al. 1998); (*iii*) daphnid biomass and production will decline due to reduction in algal biomass and production, and the shift to larger inedible forms of phytoplankton will further inhibit daphnid production (Karatayev et al. 1997; Pace et al. 1998); and (*iv*) decreased daphnid biomass and production will lead to declines in YOY fish biomass and individual specific growth (Rutherford et al. 1999).

While we hypothesized that changes in the pelagic lower trophic levels were zebra mussel induced, two alternative hypotheses explaining a decrease in phytoplankton and associated changes in other trophic levels are also possible: (*i*) reduced phosphorus loading causes a decrease in phytoplankton biomass [as Chl *a*], daphnid biomass and production, and YOY fish biomass and an increase in water clarity (nutrient limitation: bottom-up effect) or (*ii*) decreased planktivory by fish (unrelated to zebra mussels) increase zooplankton biomass leading to a decrease in both Chl *a* and primary productivity with TP remaining stable (trophic cascade: top-down effect).

Materials and methods

Study site

Oneida Lake is a 20 700-ha, shallow, productive lake (mean depth 6.8 m, maximum depth 16 m) located on the Lake Ontario Plain of central New York State (Mills et al. 1978). The lake is well mixed and generally isothermal during the ice-free months. The lake has been described as naturally eutrophic, with TP concentrations typically ranging between 30 and 60 $\mu g \cdot L^{-1}$ during the 1970s (Mills et al. 1987). Centric diatom blooms (*Cyclotella* spp.) typically have dominated early-spring phytoplankton communities, whereas cyanobacteria blooms (mainly *Aphanizomenon flos-aquae*) persist for 1 or 2 months in late summer (Greeson 1971). The zooplankton community has been dominated by two daphnid species, *Daphnia pulicaria* and *Daphnia galeata mendotae*, with smaller populations of *Daphnia retrocurva* (Mills et al. 1987). The dominant zooplanktivores are YOY fish; at high densities, YOY yellow perch are able to collapse the daphnid population (Mills and Forney 1983). Populations of gizzard shad (*Dorosoma cepedianum*) expanded in 1984 and impacted daphnid populations from the mid-1980s to the early 1990s (Roseman et al. 1996; Shepherd and Mills 1996). Zebra mussels were first observed in Oneida Lake in 1991, and by autumn 1992, the population reached densities as high as 44 000 individuals$\cdot m^{-2}$ (Mellina et al. 1995).

Limnological data

Limnological data were collected weekly at five sites (1975–1997) from April to November (Fig. 1). Sampling was conducted monthly during the winter ice-cover period (at the reference site, Shackelton Pt.; see Fig. 1). A tygon tube (2.5-cm inner diameter) was used to collect integrated water samples (surface to 0.5 m above lake bottom) for phytoplankton and nutrients. Within 2–4 h after collection, samples were filtered for Chl *a*, SRP, total soluble phosphorus (TSP), nitrate-nitrogen (NO_3), and soluble reactive silica as SiO_4 (SRS) (Strickland and Parsons 1972; American Public Health Association et al. 1976). Filtered samples were stored at a temperature of approximately –20°C prior to analysis. Unfiltered water was used to estimate TP. Dissolved organic phosphorus (DOP) was estimated as the difference between SRP and TSP and TPP as the difference between TSP and TP. Total alkalinity and phenolphthalein alkalinity of water with known pH were used to determine dissolved inorganic carbon (DIC) (Wetzel and Likens 1991).

Number of clear-water days was defined as the period between the spring and summer algae blooms when Chl *a* was less than 3 $\mu g \cdot L^{-1}$ for at least 2 consecutive weeks. In situ water column irradiance was measured with a LI-COR 4π sensor and LI-COR 1000 data logger at 0.25-m intervals from the surface to the bottom; above-surface irradiance was measured with a LI-COR 2π sensor attached to the same data logger.

Subsamples of integrated lake water from each site for phytoplankton analysis were immediately fixed in Lugol's solution upon collection and later identified and enumerated using a Wild inverted microscope. Identification was to species when possible; otherwise, phytoplankton cells were identified to genus. Biovolume estimates were determined with the use of a BASIC program (N. Idrisi, unpublished data) using average shapes and sizes for individual algal species (Reynolds 1984). All limnological, phytoplankton, and zooplankton samples were integrated over depth; thus, estimates represent water column mean values.

Primary productivity

Integrated water samples were collected for ^{14}C photosynthesis incubations using the Fee incubator technique (Shearer et al. 1985; Fee 1990). Irradiance was measured with a LI-COR 4π sensor from the surface to the bottom to determine extinction coefficients used in calculating primary productivity. Photosynthetic–irradiance (PI) experimental procedures were modified following Lewis and Smith (1983) and Fahnenstiel et al. (1995). Modifications included the incubation of a smaller sample volume (3 mL) and a 40-min incubation period. Differences in ^{14}C uptake between the two procedures were minor (Lang and Fahnenstiel 1995). Water samples were kept cool in opaque 10-L containers and transferred to the laboratory for subsequent processing; time from collection of the first sample to the return to the laboratory was typically 2 h. Prior to initial experimentation, a spectral distribution analysis was carried out at the three sampling sites with a LI-COR 1800 underwater spectroradiometer on May 18, 1993, to determine the spectral quality of the euphotic zone. A colored gel, matching the spectral distribution data, was placed at the bottom of the Fee incubator (also called a photosynthetron) between the light source and the samples to act as a filter, allowing the penetration of light wavelengths similar to those in the field.

The PI curves were fitted from photosynthetic rates at specific irradiances using the simplex nonlinear curve fitting routine in Systat 5.03 (Systat®). Two PI parameters were determined, P_m and α, from the equation (Gallegos and Platt 1981)

$$P(I) = P_m \tanh\left(\frac{\alpha I}{P_m}\right)$$

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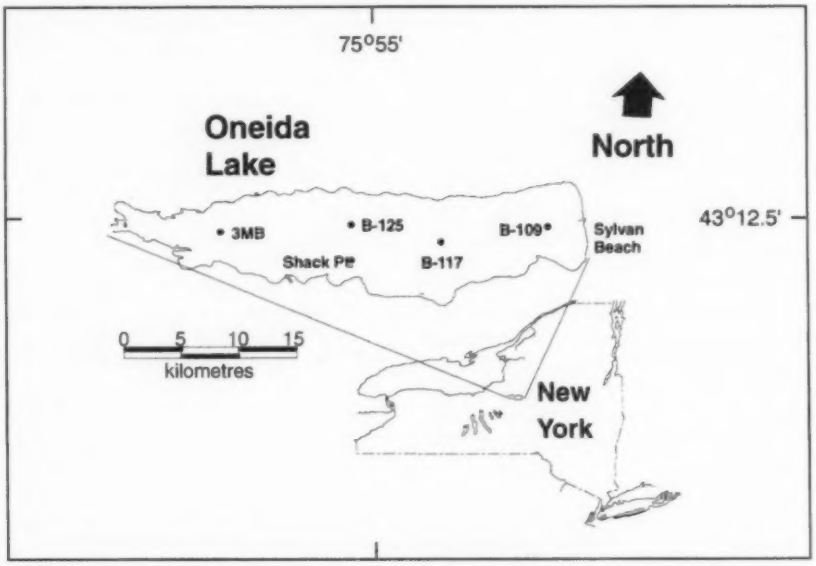
Fig. 1. Map of Oneida Lake, New York, U.S.A., showing the main sampling sites.



where $P(I)$ is photosynthetic rate (milligrams carbon per hour) at irradiance I (einsteins per square metre per hour), P_m is maximum photosynthetic rate (milligrams carbon per hour), and α is the initial linear slope at irradiance I (milligrams carbon per einstein per square metre).

Primary productivity was estimated with the computer programs developed by Fee (1990) using the PI parameters per unit chlorophyll (P_m^B(milligrams carbon per milligram Chl *a* per hour) and α^B (milligrams carbon per milligram Chl *a* per einstein per square metre)), extinction coefficients, and latitude and Julian day as input parameters. Primary productivity for years other than 1993 and 1994 was estimated using the empirical models developed in Idrisi (1997). These models, based on primary productivity measurements in 1993–1994, explained 73 and 47% of the variation for P_m and α, respectively (Idrisi 1997). The models were verified against independent data from 1988, where errors between observed and predicted PI parameters were less than 5% (Idrisi 1997).

Daphnia spp. biomass and production

Zooplankton samples were collected (at the same time and locations as the limnological and phytoplankton collections) with a 153-μm-mesh Nylon net (0.5-m mouth diameter, 2 m in length) using vertical tows from approximately 0.5 m off the sediment surface to the water surface. *Daphnia pulicaria* and *D. galeata mendotae* were enumerated and body length recorded with the use of a computer-assisted plankton analysis system (Hambright and Fridman 1994). Individual weights were calculated from length – dry weight regressions (E.L. Mills, unpublished data). Numbers of eggs per female were counted for *D. pulicaria* and *D. galeata mendotae* to estimate secondary production from 1988 to 1996 according to the method of Borgmann et al. (1984). Annual average clearance rates of daphnid populations (*D. pulicaria* and *D. galeata mendotae*) were predicted for the whole data set (1975–1997) from multivariate regressions from Peters and Downing (1984). Annual averages were calculated for the period April–October for each year using eq. 4 from Peters and Downing (1984). Input data included daphnid dry weights, food concentration (wet weight converted from Chl *a*), nanoplankton biovolumes, nanoplankton biovolumes per individual daphnid for 1975–1995, median biovolume, and biovolume per individual daphnid from Peters and Downing (1984) were used for 1996–1997.

Zebra mussel population structure

Dreissenids were collected by SCUBA using 0.5- to 1-m^2 quadrats placed randomly at each of 10 sites in triplicate (see fig. 1 in Mellina et al. 1995). Samples were collected in October of each year from 1992 to 1997; only nine sites were sampled in 1995. All individuals collected throughout this sampling period were *D. polymorpha*. Lake-wide wet weight biomass (including shell) means ± 95% confidence intervals were calculated by stratifying samples by substrate type (soft, sand, and hard substrates; Greeson 1971). Abundances and size frequency distributions were estimated for each substrate type and lake-wide estimates made by weighting abundances based on the total area of each substrate type (Cochran 1977). Because zebra mussels were not observed on any substrates deeper than 10 m, lake-wide values were corrected by assigning zero abundance for total lake bottom at depths exceeding 10 m. Annual zebra mussel clearance rates of the Oneida Lake zebra mussel population were estimated using the equations of Horgan and Mills (1997). Clearance rates were estimated as weight-specific rates based on zebra mussel dry weights (soft tissue only). We assumed that Oneida Lake was generally isothermal and well mixed during the ice-free season, and therefore, zebra mussels would have access to the entire water column. Daily clearance rates for zebra mussels were corrected for differential filtering activity between day and night (Horgan and Mills 1997).

YOY yellow perch biomass, growth, and production

Abundance of a primary zooplanktivore (yellow perch) was estimated using high-speed Miller samplers (540-μm-mesh net) in June and a 5.5-m otter bottom trawl from the end of July through October each year (1975–1997). Miller sampling was conducted when YOY yellow perch attained approximately 18 mm total length (VanDeValk et al. 1999). By the end of July, YOY yellow perch typically become demersal and vulnerable to bottom trawls (Forney 1971). Weekly estimates of YOY yellow perch from the end of July through October were obtained from trawls fished at 10 sites each week. Average daily biomass was calculated from the decline in abundance in trawl samples and observed growth rates. For the pelagic period, abundance was calculated assuming a constant instantaneous mortality rate between the date of the Miller sampling survey and the end of July (Mills et al. 1987). Average weight of YOY yellow perch in October trawls was considered to

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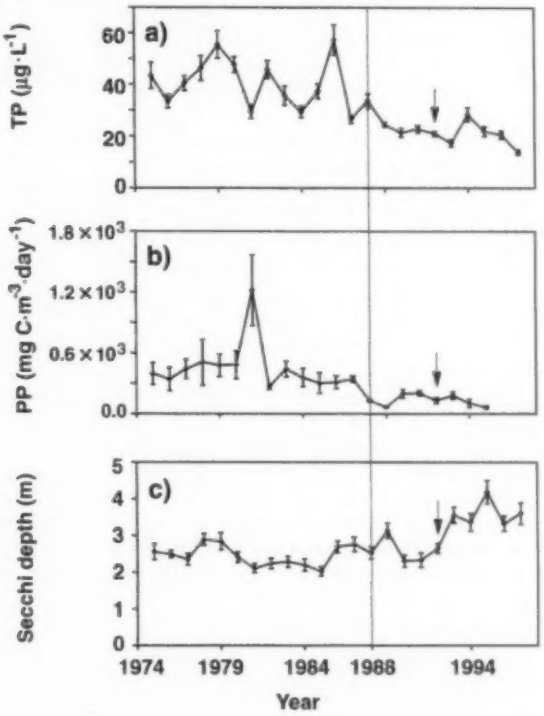
Fig. 2. Long-term trends of mean (±1 SE) annual concentrations of (*a*) TP from 1975 to 1997, (*b*) primary productivity (PP) from 1975 to 1995, and (*c*) Secchi depth from 1975 to 1997 for Oneida Lake. To the right of the vertical line drawn through all three panels is the time period used in the analysis for this study. Arrows indicate the time of zebra mussel invasion.

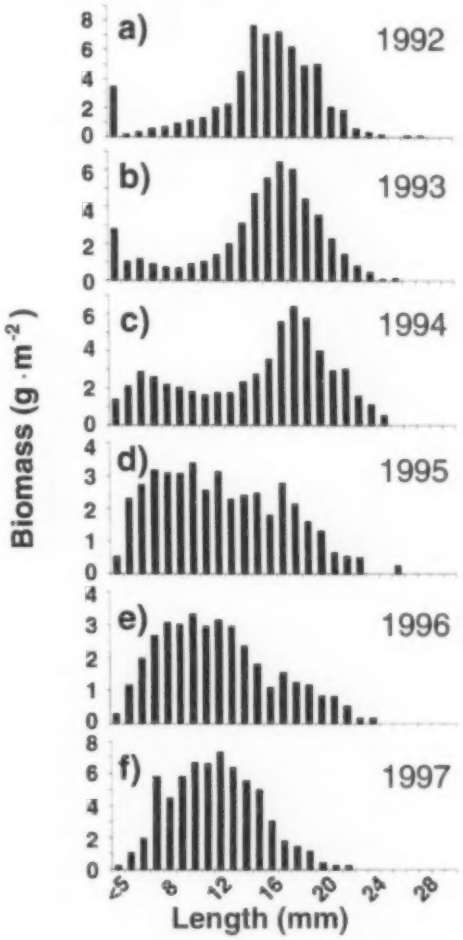


represent total annual growth. Production of YOY yellow perch was calculated from weekly changes in abundance and growth and summed to obtain annual production (Mills et al. 1987).

Data analysis

To determine the effect of zebra mussels on the lower food web, we used data from June to October of each year. This time period is when water temperature was above 10°C, and zebra mussels would most likely have the greatest impact on the system. Laboratory experiments have determined that feeding activity by *D. polymorpha* occurs at a temperature range of 8–25°C (Stanczykowska 1977); summer temperatures in Oneida Lake did not exceed 25°C during the period when zebra mussels were present. We divided the data set into pre-zebra mussel phase (1988–1991) and post-zebra mussel phase (1992–1997; we use 1992–1995 for phytoplankton biovolumes and primary productivity and 1992–1996 for daphnid production); we also grouped data for each year by season (spring, summer, and autumn). In our analysis, we did not want to confound nutrient effects with zebra mussel impacts. Consequently, we chose to begin our data analysis with 1988, since TP concentrations from 1988 to 1997 were stable; interannual differences in TP were 10–30 $\mu g \cdot L^{-1}$ for 1975–1987 compared with a maximum difference of 10 $\mu g \cdot L^{-1}$ since 1988 (Fig. 2). We used a two-way analysis of variance (ANOVA) to test for significant differences between pre- and post-zebra mussel periods followed by a comparison of means for zebra mussel phases within each season (SAS Institute Inc. 1989). When the criterion for normality was not met, we log transformed the data prior to analysis. Comparisons were considered significant at $P < 0.05$.

Fig. 3. Size frequency distributions of Oneida Lake zebra mussel population biomass from 1992 to 1997.



Results

Zebra mussel abundance and biomass

We estimated mean areal densities and wet weight of zebra mussels for each year based on numbers and weights of individuals in shell size categories ranging from <2 to 30 mm (Fig. 3). Our results indicate that mean shell length increased over the period from 2.75 (1992) to 8.72 mm (1997), maximum mean shell length was in 1995 (9.75 mm), and shell length frequencies shifted from bimodal (1992–1994) to a single mode (1995–1997). In 1992, a high abundance of small mussels (<2 mm) contributed to the highest lake-wide mean density (>40 000·m^{-2}) observed in this study. In contrast, the highest mean wet weight (including shell) of mussels was observed in 1997 (1560 g·m^{-2}) compared with average weights ranging from 343 to 1012 g·m^{-2} from 1992 to 1996. As might be expected, site-to-site variance was high; coefficient of variation among sites ranged from 84% in 1993 to 206% in 1997. Mussel densities at individual sites ranged from zero to a high of 114 300·m^{-2}

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Table 1. Statistical analysis of seasonal attributes for variables used in this study.

Parameter	Zebra mussel phase	Season
TP	ns	***
TPP	** (–)	***
SRP	ns	*
DOP	ns	ns
NO_3	ns	***
SRS	ns	*
Secchi depth	*** (+)	**
Chl *a*	* (–)	**
Primary productivity	ns	ns
Total phytoplankton	* (–)	ns
Netplankton	* (–)	ns
Nanoplankton	ns	ns
Cyanobacteria	ns	***
Diatoms	*** (–)	ns
Chlorophyta	ns	ns
Chrysophyta	*** (–)	ns
Cryptophyta	ns	ns
Mean zooplankton length	*** (+)	***
Total zooplankton	ns	*
D. pulicaria biomass	* (+)	*
D. pulicaria production	* (+)	*
D. galeata mendotae biomass	* (–)	ns
D. galeata mendotae production	** (–)	ns
Yellow perch biomass	ns	ns[a]
Yellow perch growth	ns	***[a]

Note: TP, total phosphorus; TPP, total particulate phosphorus; SRP, soluble reactive phosphorus; DOP, dissolved organic phosphorus; NO_3, nitrate-nitrogen; SRS, soluble reactive silica as SiO_2. Two-way ANOVA treatments are zebra mussel phase (pre- (1988–1991) and post-zebra mussel years (1992–1997)) and season (spring (April 1 – June 3), summer (June 10 – September 19), and autumn (September 26 – October 28)). Number of samples per group: pre-dreissenid, spring and autumn, 40; pre-dreissenid, summer, 44; post-dreissenid, spring and autumn, 60; post-dreissenid, summer, 66. The positive sign in parentheses indicates an increase during post-zebra mussel years and the negative sign indicates a decline for those variables having significant zebra mussel effects. ***$P < 0.005$; **$P \leq 0.01$; *$P \leq 0.05$; ns, not significant ($P > 0.05$).

[a]Summer and autumn values only.

and, likewise, site-to-site differences in mussel biomass (as wet weight including shell) ranged from zero to 11 276 $g \cdot m^{-2}$. Highest mussel densities were generally observed at 3 m depth, decreasing in density to depths of 7 m. No mussels were found beyond depths of 10 m.

Nutrients

We hypothesized that TP would not decline in the presence of zebra mussels but that its constituents would shift to more SRP and less TPP. Other major nutrients such as NO_3 and SRS would exhibit minimal, if any, change. Consistent with our hypothesis, we found (using a two-way ANOVA) that there was no significant difference in mean TP concentrations in pre- and post-zebra mussel years (Table 1). While SRP concentrations did not increase in the presence of zebra mussels, there was a significant decline in TPP (two-way ANOVA, $P < 0.05$). Annual averages of NO_3 and SRS concentrations exhibited no significant change in the presence of zebra mussels (Table 1).

Distributions of phosphorus and other nutrients varied significantly by season from spring to summer to autumn; TP, SRP, TPP, DOP, and SRS increased from spring to autumn, whereas NO_3 declined over the same period (Fig. 4). Comparison of phosphorus concentrations by zebra mussel phase and by season indicated that TPP was consistently lower in post-zebra mussel years for all seasons, whereas SRP and TP concentrations were lower only in summer and autumn. NO_3 was significantly lower in autumn, while SRS was lower in summer during zebra mussel years (Fig. 4).

Water clarity, Chl *a*, primary productivity, and phytoplankton community dynamics

We hypothesized that grazing by zebra mussels would lead to increased water clarity, decreased phytoplankton biomass and primary productivity, and a shift in algal composition to grazer-resistant forms. As expected, Secchi depth increased significantly (two-way ANOVA, $P < 0.05$) and Chl *a* decreased significantly (two-way ANOVA, $P < 0.05$) in the presence of zebra mussels (Table 1; Figs. 4*g* and 4*h*). The lowest annual average Chl *a* concentration was recorded in 1993 and 1997 (4.9 and 4.7 $\mu g \cdot L^{-1}$, respectively); Chl *a* was 46% lower in post-zebra mussel years. For the years 1993–1997, the annual average Secchi depth was consistently greater than that for previous years (Fig. 5*a*). Although the number of clear water days (defined as the period when mean water column Chl *a* was $<3\ \mu g \cdot L^{-1}$) increased from 60 ± 16 to 86 ± 4 days, the difference was not significant (*t* test, $P > 0.05$). This statistical outcome was likely due to the prolonged clear-water period in 1989 that extended beyond any post-zebra mussel year (Fig. 5*b*).

We found significant (two-way ANOVA, $P < 0.05$) zebra mussel effects by season for Secchi depth and Chl *a* but not for primary production (Table 1; Fig. 4). Secchi depth was greater and Chl *a* lower during post-zebra mussel years for all seasons (Figs. 4*g* and 4*h*). Primary productivity did not differ significantly (two-way ANOVA, $P > 0.05$) by season or zebra mussel presence–absence; however, higher mean primary production estimates were observed in the autumn and lower estimates in the summer in years when zebra mussels were present (Fig. 4*i*).

Primary productivity did not decline significantly during the post-zebra mussel period in spite of the significant reduction in Chl *a* (34% reduction from pre-zebra mussel Chl *a* concentrations) (Table 1; Fig. 4*i*). Primary productivity can be maintained with declining algal biomass if there is a compensatory increase in photosynthetic rate per unit chlorophyll (no observed differences in primary productivity between the two periods; *t* test, $P = 0.383$). This can occur through shifts in the PI curves or increase in light penetration. Extinction coefficient (k_D) values were significantly higher during the pre-zebra mussel period compared with post-zebra mussel years (0.742 ± 0.03 m^{-1}, and 0.564 ± 0.046 m^{-1}, respectively; *t* test, $P < 0.05$). Both α^B and P_m^B increased from pre- to post-zebra mussel years (α^B = 14.08 ± 1.68 and 20.28 ± 6.15 mg C·mg Chl $a^{-1} \cdot$einstein$^{-1} \cdot m^{-2}$, respectively; P_m^B = 6.53 ± 1.24 and 7.49 ± 1.2 mg C·mg Chl $a^{-1} \cdot h^{-1}$, respectively); however, these differences were insignificant.

Consistent with trends in Chl *a*, total phytoplankton biovolume in all seasons declined significantly after the zebra

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Fig. 4. Mean (±1 SE) seasonal (spring, summer, and autumn) (*a*) TP, (*b*) TPP, (*c*) SRP, (*d*) DOP, (*e*) NO_3, (*f*) SRS, (*g*) Secchi depth, (*h*) Chl *a*, and (*i*) primary productivity (PP) for pre- (1988–1991, open bars) and post-zebra mussel years (1992–1997, solid bars). Asterisks indicate significance levels as determined from mean comparisons of pre- and post-zebra mussel periods.

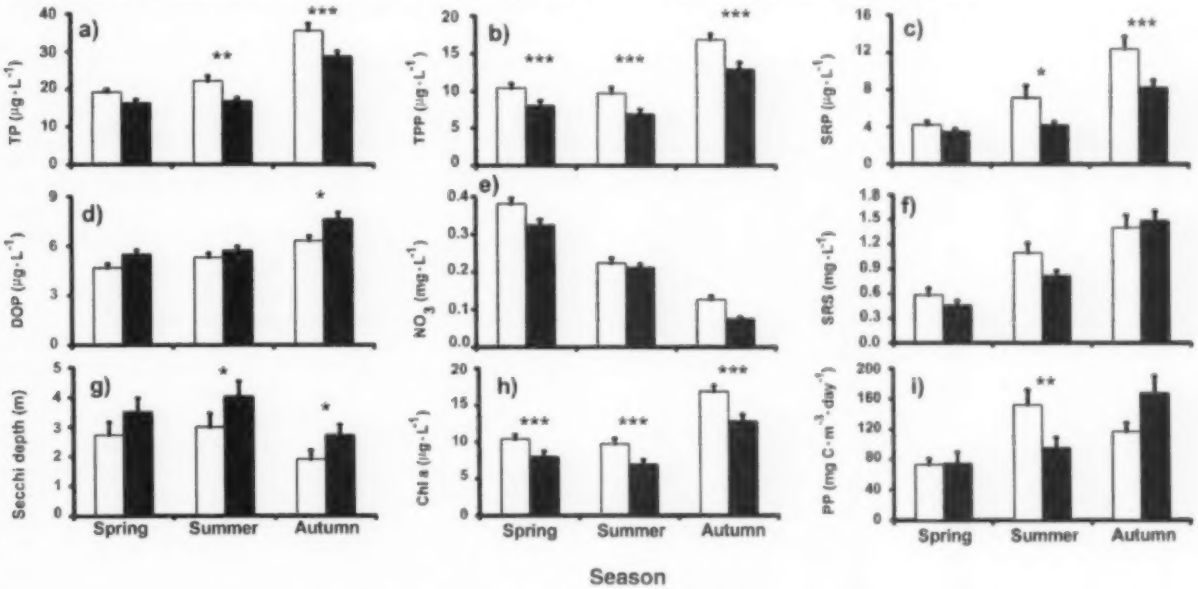
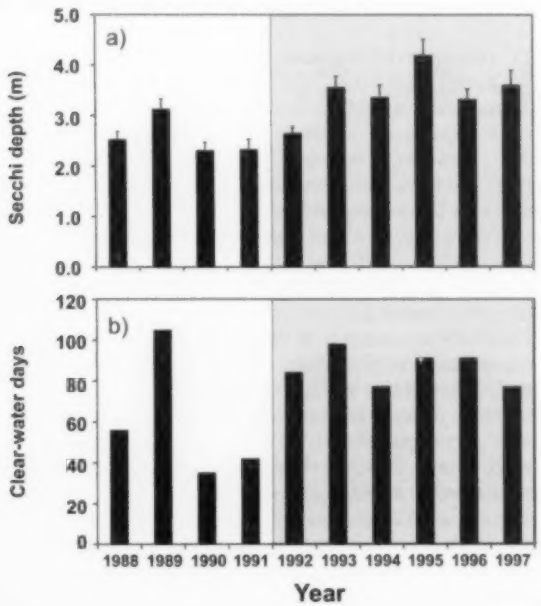


Fig. 5. (*a*) Mean annual Secchi depth (±1 SE) averaged from five sampling sites in Oneida Lake and (*b*) number of clear-water days during pre- and post-zebra mussel years. The gray shaded area indicates the post-zebra mussel period.



mussel invasion (Table 1). Associated with this decline was a shift in algal composition; the phytoplankton community structure shifted from a pre-zebra mussel community dominated by diatoms (1988–1990) to a community dominated by cyanobacteria (1992 and 1994), chlorophytes (1993), and diatoms (1995) (Fig. 6*a*). The phytoplankton community in 1991 was codominated by diatoms, cyanobacteria, and chlorophytes (Fig. 6*a*). The transitional year, 1992, was dominated by cyanobacteria but also had a higher proportion of nanoplankton than any pre-zebra mussel year (Fig. 6*b*). The nanoplankton (chlorophytes and cryptophytes) dominated the phytoplankton community in 1993, but this was followed by a dramatic decline in 1994.

Netplankton biovolume followed a trend similar to that of total phytoplankton and varied significantly with zebra mussel phase (Table 1; Fig. 7*b*). In contrast, nanoplankton did not vary significantly by zebra mussel phase in summer and autumn but did so in spring; the major difference in the spring was the dominance of the diatom *Cyclotella* spp. during the pre-zebra mussel period (Fig. 7*c*). Cyanobacteria biovolumes were not significantly different in the presence or absence of zebra mussels (Table 1; Fig. 7*d*). Diatom and chrysophyte biovolumes both declined significantly in the presence of zebra mussels, being most pronounced in the spring and autumn (Table 1; Figs. 7*e* and 7*g*). Diatoms recovered to pre-zebra mussel state in 1995 (Fig. 6*a*). Chrysophytes were extremely rare during the post-zebra mussel period in all seasons (Figs. 6*a* and 7*g*). Chlorophytes and cryptomonads were most abundant in summer during the clear-water phase; however, neither taxon varied significantly by zebra mussel phase or season (Table 1; Figs. 7*f* and 7*h*).

Daphnia spp. dynamics

We hypothesized that daphnid biomass would decline in response to a decline in algal biomass and production. *Daphnia pulicaria* and *D. galeata mendotae* were the two dominant zooplankton species throughout the study period, accounting for more than 50% of the total zooplankton community biomass (Fig. 8*b*). *Daphnia pulicaria*, the larger of the two spe-

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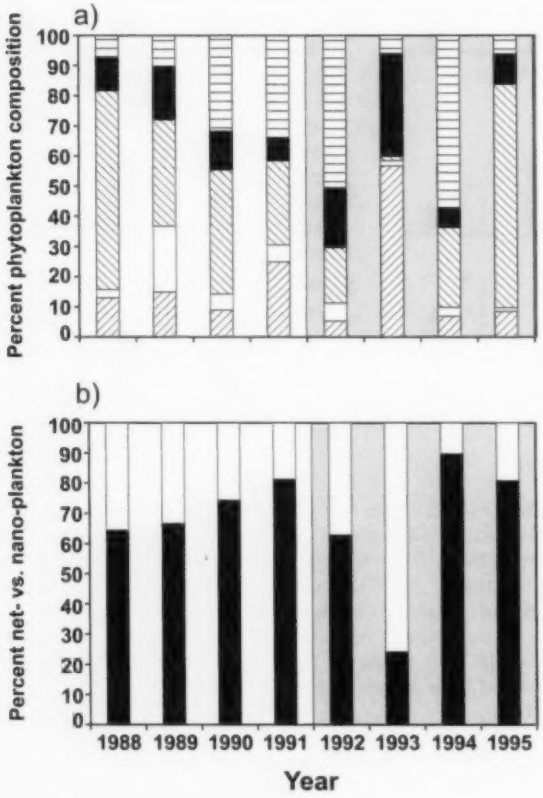
Fig. 6. Proportional annual abundance in Oneida Lake for (*a*) the five dominant phytoplankton groups (horizontally hatched bars, Cyanobacteria; solid bars, Cryptophyta; right-hatched bars, Bacilliariophyceae; open bars, Chrysophyceae; left-hatched bars, Chlorophyta) and (*b*) netplankton (solid bars) and nanoplankton (open bars) during pre- and post-zebra mussel years. The gray shaded area indicates the post-zebra mussel period.



cies, dominated the post-zebra mussel period, while *D. galeata mendotae* dominated the pre-zebra mussel period. Consistent with the dominance of the large-bodied *D. pulicaria* in post-zebra mussel years was a shift to a higher mean length of crustacean zooplankton (Fig. 8*a*). Mean zooplankton length was significantly (two-way ANOVA, $P = 0.001$) higher (39%) in years when zebra mussels were present (Fig. 9*a*). In spite of a shift to the larger *D. pulicaria* in post-zebra mussel years, total zooplankton biomass did not change significantly pre- and post-zebra mussels (Table 1). However, total zooplankton biomass was significantly greater (two-way ANOVA, $P < 0.01$) post-zebra mussels in the summer and significantly greater (two-way ANOVA, $P < 0.005$) pre-zebra mussels in the spring (Fig. 9*b*).

Mean annual *D. pulicaria* biomass and production were significantly higher in years when zebra mussels were present (Table 1; highest production estimates were in summer). Egg production may be a good indicator of feeding condition (e.g., see Pace et al. 1998 and references therein). We observed no effect of zebra mussels on combined *D. pulicaria* and *D. galeata mendotae* egg ratios (0.49 ± 0.165 and 0.502 ± 0.077 egg·individual^{-1} for pre- and post-zebra mussel years, respectively). This suggests similar feeding conditions for daphnids in pre- and post-zebra mussel periods.

Daphnia galeata mendotae exhibited no significant seasonal variation in either biomass or production but did exhibit a significant difference by zebra mussel presence–absence (Table 1). Biomass and production of this daphnid were higher in years when zebra mussels were absent; the lowest biomass and production were in the autumn during these same years (Figs. 9*e* and 9*f*). In post-zebra mussel years, biomass and production of *D. galeata mendotae* peaked in summer (Figs. 9*e* and 9*f*).

Zebra mussel and daphnid clearance rates

The most dramatic change in Oneida Lake post-zebra mussels was the temporal duration and depth of water clarity, reflected in Secchi depth and the number of clear-water days and the overall decrease in algal biovolume and Chl *a* (Figs. 4, 5, and 7). We attempted to determine if these changes were associated with clearance rates of zebra mussels and (or) daphnids. Estimated weight-specific zebra mussel clearance rates were highest in 1995 and corresponded to the highest mean shell length (9.75 mm) (Table 2; Fig. 3). Zebra mussel population clearance (as percentage of lake cleared per day) increased to its highest level (2.5 times total lake volume cleared per day) in 1997 when the population reached its highest biomass (Table 2; Fig. 3). In spite of a generally higher weight-specific clearance rate of daphnids compared with zebra mussels, daphnid population clearance rates never exceeded 8% of lake cleared per day (Table 2).

YOY yellow perch biomass, growth, and production

We hypothesized that YOY yellow perch biomass, growth, and production would decline in response to negative zebra mussel impacts on *Daphnia* spp. (also see Mayer et al. 2000). However, consistent with our findings at lower trophic levels, we observed no significant effects of zebra mussels on biomass, growth, and production of YOY yellow perch (comparisons of the years 1988–1991 and 1992–1997: two-way ANOVA, $P > 0.3$) (Tables 1 and 3). Growth rates indexed as weight in October ranged from 4.2 to 5.8 g in 1988–1991 (mean 5.2 ± 0.36 g) and from 4.5 to 8.7 g in 1992–1997 (mean 6.0 ± 0.59 g). Biomass of YOY yellow perch typically peak in July–August in Oneida Lake (Mills et al. 1987), and this was also observed for both the pre- and post-zebra mussel periods analyzed here. Production is usually greater in May–July, although neither biomass nor production was significantly different between pre- and post-zebra mussel years (Tables 1 and 3).

Discussion

Nutrient dynamics

We hypothesized that TP would not decline but would be partitioned into more SRP than TPP because of reductions in algal biomass. We did not observe a decline in TP after the establishment of zebra mussels, consistent with findings in western Lake Erie (Holland et al. 1995). Contrary to our hypothesis, however, we did not detect a significant increase in

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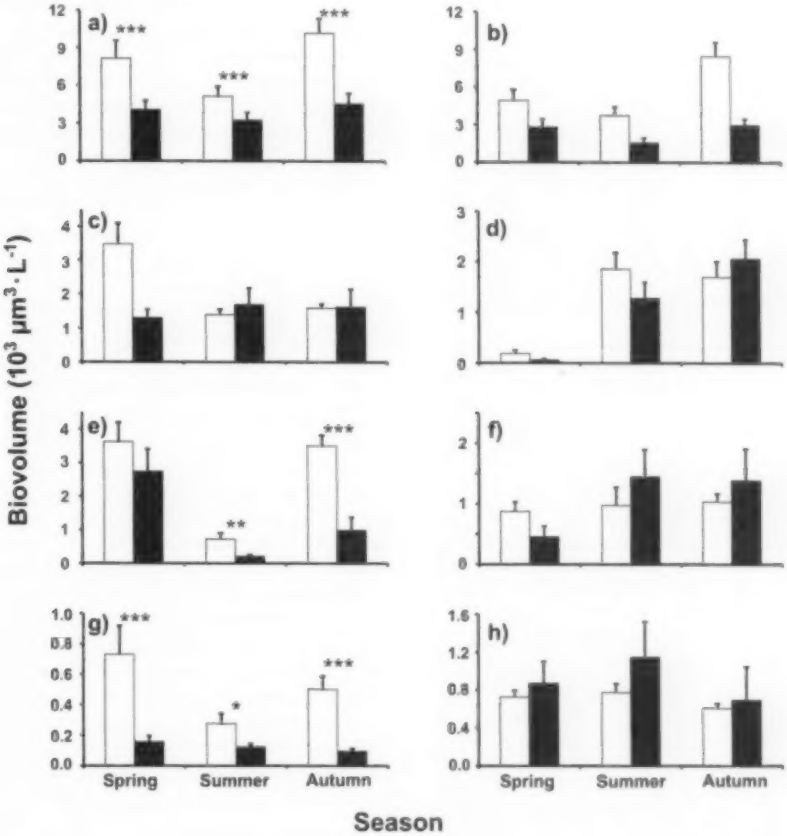
Fig. 7. Mean (±1 SE) seasonal biovolumes of (*a*) total phytoplankton, (*b*) netplankton, (*c*) nanoplankton, (*d*) Cyanobacteria, (*e*) Bacillariophyceae, (*f*) Chlorophyta, (*g*) Chrysophyceae, and (*h*) Cryptophyta for pre- (1988–1991, open bars) and post-zebra mussel years (1992–1995, solid bars). Asterisks indicate significance levels as determined from mean comparisons of pre- and post-zebra mussel periods. Note the different scales on the *y*-axis.



SRP or any change in DOP, although the DOP to TP ratio increased significantly (0.218 ± 0.026 and 0.302 ± 0.02 pre- and post-invasion, respectively; *t* test, $P = 0.033$) during post-zebra mussel years. While these results are consistent with those observed in Saginaw Bay (Johengen et al. 1995), they differ from those of recent studies in the Hudson River where SRP exhibited a significant increase (150%) and in western Lake Erie where SRP increased by 17% (Holland et al. 1995). In contrast with SRP, DOP concentrations were higher in the autumn in years when zebra mussels were present (but not in spring and summer). Heath et al. (1995) found higher DOP concentrations in enclosures with high densities of zebra mussels, although the results were confounded due to unusually high concentrations in one of the control enclosures. Short-term increases in phosphorus concentrations have been shown in laboratory and mesocosm experiments to be attributed to excretion by zebra mussels (Heath et al. 1995; Mellina et al. 1995; Arnott and Vanni 1996). The influence of zebra mussel excretion on phosphorus cycling, however, depends on zebra mussel population size, size of individual mussels, and the relative concentration of phosphorus in the water column (e.g., Heath et al. 1995; Mellina et al. 1995; Arnott and Vanni 1996); these conditions may account for the different responses in phosphorus dynamics among freshwater ecosystems. In any case, the lack of change in TP in Oneida Lake suggests that potential productivity has remained unchanged, and this finding may help explain why production at other trophic levels exhibited little or no change in response to zebra mussels.

Water clarity, Chl *a*, primary productivity, and phytoplankton community structure

Observed changes in Secchi depth, Chl *a*, and phytoplankton biovolume were consistent with our hypothesis that phytoplankton biomass (and Chl *a*) would decline as water clarity increased in response to grazing by zebra mussels, as observed elsewhere (e.g., Holland 1993; Karatayev et al. 1997; Strayer et al. 1999). However, primary productivity did not decline as predicted. Higher PI parameter values and lower extinction coefficients may have compensated for low chlorophyll concentrations.

Primary productivity cannot be maintained if algal biomass declines unless there is a compensatory increase in production per unit biomass (Fahnenstiel et al. 1995). This in turn can be caused by an enhanced light environment or by changes in the phytoplankton community to species with

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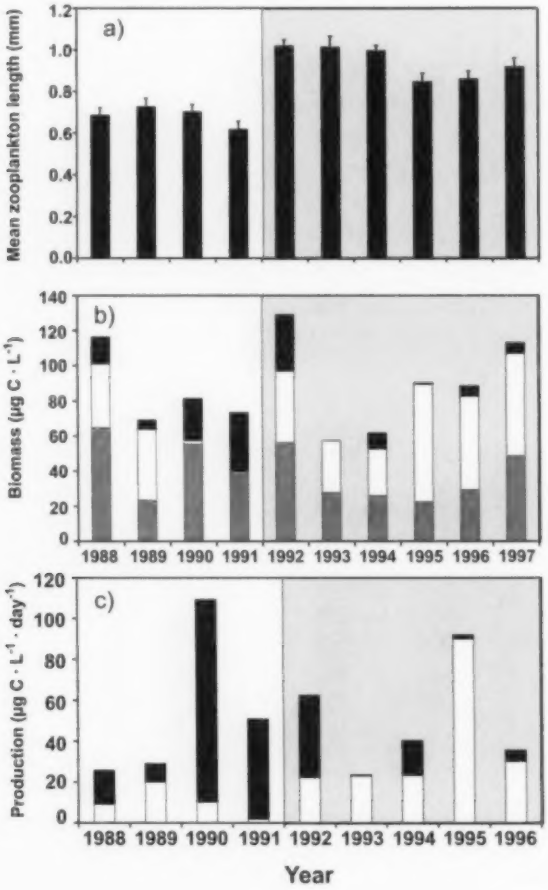
Fig. 8. (*a*) Annual mean (±1 SE) zooplankton lengths, (*b*) annual biomass of *D. galeata mendotae* (open bars), *D. pulicaria* (solid bars), and other zooplankton species including other cladocerans and copepods (gray bars), and (*c*) annual production of *D. galeata mendotae* (open bars) and *D. pulicaria* (solid bars) during pre- and post-zebra mussel years (gray shaded area).



higher growth rates. In Oneida Lake, changes in PI parameters between pre- and post-zebra mussel periods were in the direction of higher efficiency per unit chlorophyll; also, increased water clarity accounted for higher photosynthetic rates below 5 m depth. For example, areal primary production at Station B-125 on May 24, 1993, was 183 mg C·m^{-2}; using the proportional changes in P_m^B, α^B, k_D, and Chl *a* that occurred between pre- and post-zebra mussel years and assuming 20% variation to determine significant differences, we find no change in areal primary production (184 mg C·m^{-2}) if Chl *a* is reduced to 65% of the original concentration. The observed changes in parameters that affect primary production require a reduction of Chl *a* by at least 50% in order to produce a significant decline in primary production (141 mg C·m^{-2}). In other systems, the compensatory effects of increased water clarity and photosynthesis were not sufficient to compensate for the dramatic declines in Chl *a* concentration, which were greater than those observed in Oneida Lake (e.g., Fahnenstiel et al. 1995; Caraco et al. 1997). The degree of compensation will likely vary among systems depending on the combination of factors, including PI parameter values, light environment, phytoplankton species composition, and Chl *a* concentration.

The response of algal communities to dreissenid grazing varies among freshwater ecosystems (Smith et al. 1998; Makarewicz et al. 1999). In Oneida Lake, a short-term shift was observed in the phytoplankton community to more nanoplankton (Chlorophyta, Cryptophyta, and *Cyclotella* spp.) and less netplankton (Bacillariophyceae, Chrysophyceae, and Cyanobacteria). However, annual variability was high, thus precluding the observation of any clear trends in phytoplankton dynamics over the long term. A clear shift, however, occurred in the Hudson River where there was a marked decline in cyanobacteria and a relative increase in diatoms postinvasion (Smith et al. 1998). It is argued that the likely cause for the relative increase of diatoms over cyanobacteria (dominated by *Microcystis* spp. in the Hudson River) was the differential growth rates of phytoplankton in response to zebra mussel grazing (Smith et al. 1998).

On the other hand, Arnott and Vanni (1996) hypothesized that low nitrogen to phosphorus ratios (a result of zebra mussel excretion) could cause a shift in the phytoplankton community to cyanobacteria due to nitrogen limitation. Although we do not have nutrient data comparable with those of Arnott and Vanni (1996), NO_3 and SRP concentrations indicate possible nitrogen limitation in Oneida Lake since 1985 during the summer and autumn. Consequently, late-summer nitrogen limitation leading to cyanobacteria blooms in Oneida Lake likely preceded the invasion by zebra mussels. Makarewicz et al. (1999) found a significant increase in cyanobacteria in the western basin of Lake Erie in the spring, but this was followed by a significant decline in the summer. There were no significant differences in cyanobacteria biovolumes in all seasons analyzed in Oneida Lake.

Daphnid community

We predicted that zebra mussels would negatively impact *Daphnia* spp. biomass and production in response to lower algal food resources. Our findings do not support this hypothesis. Although algal food resources declined, *Daphnia* spp. biomass and production did not decline significantly. We attribute the persistence of the daphnid community to our observation that primary production did not change significantly (probably due to increased water clarity; see above) and that there was no shift to less edible algal species; this result was also predicted in a simulation model (Padilla et al. 1996). Pace et al. (1998) similarly found that macrozooplankton did not significantly decline after the zebra mussel invasion in the Hudson River. Microzooplankton were significantly reduced in the Hudson River (Pace et al. 1998) but were not sampled efficiently with the 153-µm-mesh net used in Oneida Lake.

The daphnid species shift observed in Oneida Lake was not studied in the Hudson River, although Pace et al. (1998) speculated that a shift in species composition might have occurred. *Daphnia galeata mendotae* tend to dominate in years of high planktivory by fish in Oneida Lake (Mills and Forney 1983). Large year-classes of gizzard shad occurred in 1990 and 1991, leading to high planktivory rates and a dominance of *D. galeata mendotae* over *D. pulicaria* (Roseman

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Fig. 9. Mean (±1 SE) seasonal values of (*a*) mean zooplankton length, (*b*) total zooplankton biomass, (*c*) *D. pulicaria* biomass, (*d*) *D. pulicaria* production, (*e*) *D. galeata mendotae* biomass, and (*f*) *D. galeata mendotae* production (the post-zebra mussel years for *D. pulicaria* and *D. galeata mendotae* production included 1992–1996) for pre- (1988–1991, open bars) and post-zebra mussel years (1992–1997, solid bars). Asterisks indicate significance levels as determined from mean comparisons of pre- and post-zebra mussel periods.

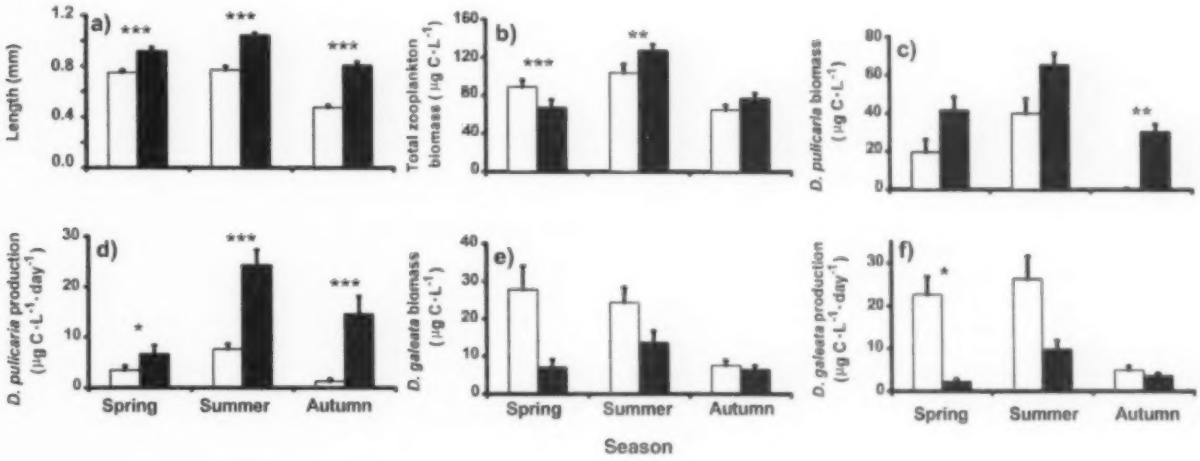

Table 2. Annual average clearance rates and proportion of lake cleared per day for total populations of daphnids (*D. pulicaria* and *D. galeata mendotae*) and zebra mussels in Oneida Lake.

Year	Daphnid (mL·mg dry weight^{-1}·day^{-1})	Daphnid (% lake cleared·day^{-1})	Zebra mussel (mL·mg dry weight^{-1}·day^{-1})	Zebra mussel (% lake cleared·day^{-1})
1975–1991	243	3	—	—
1992	430	8	15.5	180
1993	261	2	116	189
1994	262	3	287	198
1995	407	8	302	149
1996	305	6	296	132
1997	398	7	298	249

Note: Pre-zebra mussel clearance rates and proportion of lake cleared of daphnids are averages for the period 1975–1991.

et al. 1996; Shepherd and Mills 1996), but large numbers of these fish were not observed post-1992 (VanDeValk et al. 1999). Larger daphnids may be better competitors at low food levels (Gliwicz 1990), and this has been used to explain the dominance of *D. pulicaria* in years when planktivory rates are low (Rudstam et al. 1993). Zebra mussels could induce low food levels, leading to the dominance of *D. pulicaria*. However, in 1998 and 1999, *D. galeata mendotae* was again the dominant species, even though algal biomass did not increase (E.L. Mills, unpublished data). In those years, a resurgence of emerald shiner (*Notropis atherinoides*) and an associated increase in pelagic planktivore biomass likely caused the shift back to the smaller daphnid (VanDeValk et al. 1999). Thus, we believe that the observed shift in *Daphnia* spp. composition associated with zebra mussels was due to the concomitant decline in open-water planktivory by gizzard shad rather than a zebra mussel effect of reduced resources.

Yellow perch

Consistent with our observations in the daphnid community, we did not detect a decrease in YOY yellow perch growth, biomass, and production following the establishment of zebra mussels. Mayer et al. (2000) reported an increase in YOY yellow perch growth post-zebra mussels in their study of Oneida Lake (1964–1997). Although we also observed an increase in YOY yellow perch growth post-zebra mussels, this increase was not significant, probably because the power of our analysis was lower (4 versus 27 pre-zebra mussel years). Mayer et al. (2000) found increased YOY yellow perch growth after accounting for density-dependent effects and attributed such growth to increased feeding efficiency on zooplankton (mainly daphnids) associated with zebra mussel induced elevated water clarity. Increased YOY yellow perch growth could not be attributed to the presence of zebra mussel veligers. These veligers are smaller (90–200 mm; Sprung 1993) than prey generally consumed by larval yellow perch (Schael et al. 1991), and diet analysis from two post-zebra mussel years showed no veligers in YOY yellow perch diets (Mayer et al. 2000).

In conclusion, our findings suggest that compensatory factors have lessened the impact of *D. polymorpha* on the pe-

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Table 3. Mean (±1 SE) seasonal YOY yellow perch biomass, daily specific growth rate, and production for pre- (1988–1991) and post-zebra mussel years (1992–1997).

Variable	Zebra mussel phase	Season	
		Summer	Autumn
Biomass (mg wet weight·m^{-3})	Pre	41.8±3.94	23.6±2.6
	Post	37.2±4.29	26.8±3.5
Specific growth rate (mg wet weight·day^{-1})	Pre	1.1±0.203	4.7±0.119
	Post	1.4±0.203	6.0±0.179
Production (kg wet weight·ha^{-1}·season^{-1})	Pre	12.6±5.5[a]	7.06±3.15[b]
	Post	9.6±2.3[a]	9.02±2.17[b]

[a]May 27 – July 15.
[b]July 15 – October 14.

lagic lower food web of Oneida Lake. Light appears to be a crucial factor, allowing phytoplankton production deeper in the water column. It appears that low food resources did not impact the daphnid community and that this community is more sensitive to top-down pressure from planktivores (Mills and Forney 1983). Consistent with these findings, we found no evidence that zebra mussels had a negative impact on young yellow perch production. While our analysis has focused on the short-term impacts of zebra mussels on the pelagic food web of Oneida Lake, the long-term effects of zebra mussels is yet to be determined. In a long-term European study (40+ years; Karatayev et al. 1997), the zebra mussel invasion caused an increase in water clarity and macrophyte and zoobenthos biomass and a decrease in phytoplankton and zooplankton biomass. However, after approximately 10 years, zebra mussel impacts were less pronounced but the lake ecosystem did not revert to pre-zebra mussel conditions. Whether Oneida Lake follows a pattern similar to that of Lake Lukomske will only be ascertained through continued and rigorous study of the pelagic food web in the coming decades.

Acknowledgments

The authors are deeply indebted to the many people who contributed to the sampling program and data analysis spanning over two decades at the Cornell Biological Field Station. We wish to thank M. Olson, G. Fahnenstiel, G. Sprules, O. Johannsson, S. Millard, S. Smith, and many others for discussions, suggestions, and ideas during the course of this study as well as two anonymous referees for their constructive comments on an earlier version of the manuscript. This paper is a result of research funded by National Oceanic and Atmospheric Administration award NA46RG0090 to the Research Foundation of State University of New York for New York Sea Grant. The U.S. government is authorized to produce and distribute reprints for government purposes, notwithstanding any copyright notation that may appear herein. The views expressed herein are those of the authors and do not necessarily reflect the views of the National Oceanic and Atmospheric Administration or any of its subagencies. The New York Department of Environmental Conservation provided support to the Cornell Warm Water Fisheries Unit (Federal Aid Project FA-5-R). Contribution No. 196 of the Cornell Biological Field Station.

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Prey capture ability of mummichogs (*Fundulus heteroclitus*) as a behavioral biomarker for contaminants in estuarine systems

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Abstract: Prey capture was evaluated as a behavioral biomarker of contamination by examining feeding behavior of adult mummichogs (*Fundulus heteroclitus*) from 13 sites. Prey capture ability was related to sediment and tissue contaminant levels and with previous genetic analyses. The levels of contaminants at a site were highly correlated with each other, confounding the impacts of individual contaminants. The number of prey (grass shrimp) captured was highest in three of the cleanest sites. Sites with the lowest capture rates were generally more contaminated. The number of captures at all sites was highly variable, with both high and low efficiencies in highly contaminated populations. A significant relationship exists between the *Mdh-A(a)* allele and captures, with higher captures in the southern populations. Gut content analysis of field-collected fish had grass shrimp as the largest proportion of the diet at sites whose fish had the highest laboratory capture rates. Thus, prey capture as a behavioral biomarker is ecologically relevant and corresponds to diet in the field. However, it is not especially sensitive due to great variability at each site. Behavioral differences related to overall contaminant levels rather than to specific toxicants.

Résumé : On trouvera ici une évaluation de la capture des proies comme biomarqueur comportemental de la contamination par l'examen du comportement alimentaire des Choquemorts (*Fundulus heteroclitus*) adultes à treize sites. La capacité de capturer des proies a été mise en relation avec les concentrations de contaminants dans les sédiments et les tissus et avec les résultats d'analyses génétiques antérieures. Les concentrations de contaminants à un site sont en forte corrélation les unes avec les autres, ce qui masque l'impact des contaminants individuels. Le nombre de proies (crevettes bouquets) capturées est maximal aux trois sites les plus « propres ». Les sites dans lesquels les captures sont minimales sont généralement plus contaminés. Le nombre des captures à tous les sites est hautement variable, avec à la fois des efficacités élevées et basses de capture chez des populations fortement contaminées. Il existe une relation significative entre la présence de l'allèle *Mdh-A(a)* et les captures et ces dernières sont plus importantes chez les populations plus australes. L'analyse du contenu du tube digestif de poissons récoltés en nature montre que les crevettes bouquets représentent la majorité des proies aux sites dont les poissons possèdent les plus forts taux de capture en laboratoire. La capture des proies commne biomarqueur comportemental est donc d'intérêt écologique et elle correspond à l'alimentation en nature. Ce n'est cependant pas un marqueur particulièrement sensible à cause de la grande variabilité à chacun des sites. Les différences comportementales sont reliées aux niveaux globaux de contamination plutôt qu'à des substances toxiques particulières.

[Traduit par la Rédaction]

Introduction

Contaminants can alter behavior, including predator–prey interactions, which can have effects on food webs. Atchison et al. (1987) reviewed the effects of metals on fish behavior, including locomotion, attraction and avoidance, swimming performance, respiratory behavior, learning, social interactions, reproductive behavior, feeding, and predator avoidance. They emphasized that studies should have ecological relevance, and that observations made in the laboratory should be validated in the field.

Reduced feeding is a common response to contaminants. It can lead to reduced energy intake, which can easily be worked into energy budget models to predict consequences

Received August 15, 2000. Accepted April 27, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 21, 2001.
J15922

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 DOI: 10.1139/cjfas-58-7-1442 © 2001 NRC Canada

at the population level (Maltby 1999). Reduced feeding behavior, which can retard growth and decrease survival in larval rainbow trout (*Oncorhynchus mykiss*), could be separated into different processes, such as motivation, orientation to prey, strikes, size-selectivity, and miscues (Little et al. 1990). Impaired feeding behavior in rainbow trout and lake trout (*Salvelinus namaycush*) was noted in response to exposure to sublethal concentrations of various pollutants (Little et al. 1990; Scherer et al. 1997), and can be related to impaired growth and population declines. Pollutants may impair feeding behavior by affecting the motivation to feed and (or) by reducing the ability to capture prey. Little et al. (1990) noted that the frequency of strikes was less sensitive to certain toxicants than the actual prey capture, indicating that coordination was impaired. However, Brown et al. (1987) found that largemouth bass (*Micropterus salmonoides*) treated with pentachlorophenol (PCP) performed fewer strikes, reflecting decreased motivation to feed. Prey handling time by bluegills (*Lepomis macrochirus*) can be increased by toxicant exposure, and can contribute to lowered feeding rates (Sandheinrich and Atchison 1989). By altering feeding, pollutants can change predator–prey interactions, and thus populations.

The mummichog, *Fundulus heteroclitus*, is a very abundant estuarine fish that consumes primarily crustaceans and annelids, and feeds on the marsh surface at high tide. Adults are prominent predators of the grass shrimp, *Palaemonetes pugio* (Kneib 1986), which is also very abundant in East Coast tidal marshes. Mummichogs also consume detritus, although it is of little nutritional value (Prinslow et al. 1974) and may be incidental while foraging for live food. *F. heteroclitus* is eaten by migratory fishes, such as white perch (*Morone americanus*) and striped bass (*Morone saxatilis*), as well as by the blue crab, *Callinectes sapidus* (Kneib 1987).

There is considerable genetic variation in *F. heteroclitus*: there are two subspecies that differ in egg morphology and spawning site preference (Able and Felley 1986) and in the frequency of various allozyme markers including Ldh-B, Mdh-A, and Gpi-B (Powers et al. 1986), some of which exhibit very steep clines. *F. heteroclitus heteroclitus* is found south of northern New Jersey (NJ), U.S.A., while *F. h. macrolepidotus* occurs to the north. Recent work (Weis et al. 1999) using allozyme frequencies and mitochondrial DNA suggests that the two subspecies are separated by a 120–150 km area, inhabited by an intermediate form with the northern mtDNA and transitional frequencies of *Mdh* alleles. This intermediate group inhabits the chronically polluted New York – New Jersey Harbor Estuary system.

Previous studies demonstrated differences between mummichog populations from clean reference areas and contaminated areas, notably Piles Creek (PC), a polluted tributary of the Arthur Kill in Linden, N.J. Surrounded by industrial sites, a sewage treatment plant, a power plant, and a major highway, the sediments and biota of this creek have elevated levels of many contaminants (Eckenfelder Inc. 1991). PC fish have reduced growth and a shorter lifespan compared with those from cleaner sites in eastern Long Island, New York (NY), and Tuckerton (TK) N.J. (reviewed in Weis and Weis 1989). The population has fewer large individuals and is considerably less dense than the one at TK (Santiago Bass et al. 2001). Nevertheless, the population persists because of compensation via increased reproductive effort (Weis and Weis 1989).

In experiments using the grass shrimp, *P. pugio*, as prey, PC fish were poor predators compared to fish from TK (Smith et al. 1995). Videotape analysis showed that the poor prey capture was primarily due to fewer attempts to capture prey, rather than to poor coordination (Smith and Weis 1997). PC fish, being generally "slow," had lower spontaneous activity and were more vulnerable to predation by blue crabs than TK conspecifics (Smith and Weis 1997). The reduced growth of PC fish is associated with a lower prey capture ability (Smith and Weis 1997). Impaired prey capture was also seen in fish that had been exposed to (Hg) in the laboratory for one week (Weis and Khan 1990). The poor predation by PC fish was correlated with elevated brain Hg. When TK fish were maintained in an aquarium with PC sediments and water and fed PC grass shrimp, their prey capture ability declined to that of PC fish in one month and their brain Hg level increased to that of the PC fish. When PC fish were maintained in clean water for two months, there was only a slight improvement in their prey capture ability, and brain Hg did not decrease (Smith and Weis 1997). This correlation of behavior with brain Hg does not necessarily mean that Hg causes the altered behavior; other contaminants may contribute, and there are many at PC. In aquatic systems, it is difficult to establish causal relationships between particular contaminants and effects, due to the multitude of interacting environmental factors.

Biomarkers, which can provide information about exposures to contaminants or sublethal effects resulting from such exposures, are typically at the biochemical or cell level of biological organization. Thus, their links to population level effects are difficult to establish. If altered behavior should prove to be a useful biomarker, its links to population level effects are much more apparent and direct. Furthermore, behavioral investigations are non-destructive. The present study was designed to investigate a larger number of populations from areas with different levels of various contaminants, to examine behavioral differences, and to narrow the field of potential contaminants responsible for reduced prey capture. Considering prey capture a behavioral biomarker of contaminant effects, we examined feeding behavior of adult mummichogs from many different sites, including some severely contaminated ones as well as reference areas. We attempted to relate prey capture ability with sediment and tissue (liver and brain) contaminant levels. These results were related to genetic analyses done previously to see if behavioral differences might have a (partly) genetic origin. Gut contents of additional field-collected specimens were investigated to see if the actual diet in the field related to the behavior observed in the laboratory: a field validation.

Materials and methods

Fish were collected using minnow traps at the sites described in Table 1. Every site had data on behavior and contaminants collected. At most but not all sites, we obtained data on gut contents. Metals were measured in the livers and brains of fish from most sites. Sediment analyses were done on sediments for most sites.

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Table 1. Collection sites.

Genotype	Site	Abbrev.*	Description	State
Northern	New Bedford Harbor	ND	PCB Superfund site	Mass.
	West Island	WI	Reference site near New Bedford	Mass.
	Foundry Cove	FC	Former Cd Superfund site on the Hudson River	N.Y.
Intermediate	Sandy Hook	SH	Entrance to Raritan Bay	N.J.
	Newark Bay	NB	Highly contaminated urban estuary	N.J.
	Piles Creek	PC	Highly industrialized, off the Arthur Kill in Linden, N.J.	N.J.
	Vince Lombardi Rest Stop	VL	Northern part of the contaminated Hackensack Meadowlands, adjacent to the N.J. Turnpike	N.J.
	Union Beach	UB	Southern edge of Raritan Bay	N.J.
	Berry's Creek	BC	Hg Superfund site in the Hackensack Meadowlands	N.J.
	Bullhead Bay	BB	Relatively clean site in Southampton, previously used as a reference site but near a golf course	N.Y.
	East Hampton	EH	Accabonac Harbor, a clean reference site	N.Y.
Southern	Tuckerton	TK	Clean reference site	N.J.
	Scuffletown Creek	SC	Across the Elizabeth River from the Atlantic Wood PAH Superfund site, near Norfolk	Va.

Note: PCB, polychlorinated biphenyls; PAH, polynuclear aromatic hydrocarbons.
*Abbreviations used in text.

Contaminants

Sediments

Sediment samples of the top 5 cm in shallow subtidal areas from each of the sites, two replicates per site, were collected in acid-washed polycarbonate jars and stored at 4°C until analyzed. They were dried, weighed, and extracted with 3:1 nitric acid – perchloric acid reagents at 70°C for 24 h. The extracts were analyzed for Cd, Pb, Cu, and Zn by atomic absorption spectrophotometry (AA) by flame absorption in a Perkin-Elmer model 603 instrument. For Hg analyses, cold vapor AA methods of Hatch and Ott (1968) were used: 4:1 H_2SO_4–HNO_3 extraction, overnight $KMnO_4$ oxidation, NH_2OH HCl and $SnCl_2$ reduction, and measurement in a Bacharach MAS-50D instrument. In addition to the data we collected, we utilized existing sediment data on organic contaminants, collected at or near these sites by other investigators, such as the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP) (Eckenfelder Inc. 1991; Nelson et al. 1996; Adams et al. 1998).

The Effects Range – Low (ER-L) and Effects Range – Medium (ER-M) values (Long et al. 1995) reflect sediment contaminant levels that may cause adverse effects. To assess overall contamination, the sediment concentration of each contaminant at each site was divided by its ER-L to generate an ER-L equivalent. Thus, if the concentration of a given contaminant in the sediments were twice the ER-L, the ER-L equivalent would be 2. For each site, the ER-L equivalents for the different contaminants were then added up to create an index of total contamination, expressed as ΣER-L. In a similar way, ER-M equivalents were calculated for each contaminant (ΣER-M).

Contaminants in fish tissue

Fish were collected and frozen at –80°C upon return to the laboratory. The liver and brain of each fish was removed (pooled samples, 3 replicates per site), weighed, dried to constant weight, re-weighed, digested in 3:1 HNO_3–$HClO_4$ and the metals analyzed by AA in a Perkin-Elmer 503 with an autosampler, using graphite furnace methodology. For Hg analysis, the same cold vapor AA procedure was used as for sediment.

Quality assurance for the metal analyses involved simultaneous analyses of NIST (National Institute of Standards and Technology) standard reference material SRM 1645 (Estuarine Sediment) for sediment analysis and NRCC (National Research Council Canada) certified reference material DORM-2 (dogfish muscle) for fish tissue analysis, as well as method blanks. One reference material and one blank was included with every 12 samples. Acceptability of data for a run required the reference data to be within the 95% confidence limits; this was usually met except for Cr in the estuarine sediment standard, but this was not a certified element. Acid-washed glassware, deionized/distilled water, and reagents for trace metal analysis were used throughout.

Prey capture

Adult fish (60–80 mm standard length (SL)) were collected with traps or seines and acclimated to the laboratory for a week while being fed flake food. Sixty fish from each site were tested in groups of three (N = 20 per site) for prey capture by using 10 grass shrimp (*P. pugio*) in 80-L aquaria in 15‰ sea water with three opaque sides and three large rocks on the bottom to serve as prey refuges, as per Smith and Weis (1997). Fish were observed for 30 min and the number of strikes and number of prey captured were recorded every 5 min. We report only the 30-min captures.

Gut contents

Samples of adult mummichogs (>60 mm SL) collected from the field were taken during outgoing tides (since fish feed at high tide on the marsh surface) using unbaited minnow traps. After CO_2 narcosis, fish were preserved in 10% formalin. Digestive tracts were removed from 30–50 adults per site, and the contents separated, identified as far as possible, dried to constant weight and weighed on an analytical balance. The weights of grass shrimp, detritus and other components were taken and their percentages of the total weight of the gut contents calculated.

Data analysis

Predation behavior was summarized by site as mean number of captures per trial and mean efficiency (captures/strikes). The observed distribution of contaminant levels in fish tissue and sediment were plotted, and bivariate linear (r) and Spearman rank (r_S) correlations among contaminants and adult predation behaviors were computed. Correlations among sediment, brain and liver contaminants were expressed as linear (r) and Spearman rank (r_S) correlations, with one measurement per site. When indicated by preliminary plots, contaminant measurements were transformed to a log scale; a log value one-half the next smallest value was

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Table 2. Metals levels measured in the sediments ($\mu g \cdot g^{-1}$, mean ± standard deviation) from the various sites.

Site	Hg	Cu	Pb	Zn	Cd	Total PCB	Total PAH
BB	0.01 ± 0.005	47.5 ± 6.3*	134 ± 1.4	189 ± 114*	2.4 ± 0.56*	0.003	0.44
BC	206 ± 7.7**	347 ± 29.7**	273 ± 9.2**	1693 ± 113**	18.6 ± 0.7**	0.7**	12.8*
EH	0.006 ± 0.002	31.5 ± 0.7	24.5 ± 2.9	66 ± 5.6	1.2 ± 0.14	0	0.08
FC	0.046 ± 0.005	50 ± 1.6*	52.7 ± 1.8*	185 ± 9.4*	6.5 ± 0.11*	0.61**	4.6*
NB	0.46 ± 0.23*	634 ± 277**	1020 ± 836**	851 ± 308**	5.5 ± 2.3*	0.63**	27.4*
ND	0.40 *	450**	130*	260*	12**	8.2**	
PC	6.3 ± 1.0**	485 ± 46.7**	107 ± 20.8*	525 ± 67.1**	7.1 ± 2.1	0.69**	22.8*
SC	0.66 ± 0.005*	215 ± 14.1*	189 ± 13.4*	622 ± 10.6**		0.2**	4
SH	0.02 ± 0.005	113 ± 84*	285 ± 147**	181 ± 79*	1.6 ± 1.3	0.006	0.63
TK	0.19 ± 0.02*	43.8 ± 7.6*	73.2 ± 8.0*	141 ± 13.4	2.1 ± 1.2	0.25**	6.0*
UB	0.03 ± 0.005	112 ± 8.5*	150 ± 12.7*	284 ± 2.8*	1.7 ± 2.4*	0.11*	17.1*
VL	0.36 ± 0.17*	144 ± 37*	221 ± 104**	337 ± 47.4*	3.4 ± 0.1		62**
WI	0.07	19	18	42	0.28	0.83*	
ER-L	0.15	34	46.7	150	1.2	0.023	4.02
ER-M	0.71	270	218	410	9.6	0.18	44.79

Note: Selected organic contaminants in sediments ($\mu g \cdot g^{-1}$), taken from EPA data. See Table 1 for site names and descriptions. PCB, polychlorinated biphenyls; PAH, polynuclear aromatic hydrocarbons. ER-L and ER-M values (Long et al. 1995) are included at the bottom of the table for reference. Data with * exceed the ER-L, those with ** exceed the ER-M.

imputed to 0 values. The number of captures was treated as a Poisson variate. Analysis of variance (ANOVA) was performed to compare sites, after square root transformation of captures, to normalize and stabilize the variance of the Poisson variate. Tukey's adjustment for pairwise comparisons was used. The association of contaminants with captures was analyzed by Poisson regression using the GENMOD SAS procedure, with estimates and p-values adjusted for overdispersion (greater within-site variability in responses than a simple Poisson variable.) Generalized coefficients of determination (r_G) were used to express the degree of correlation between captures and contaminants, following Nagelkerke's procedure as computed in SAS modules (SAS Institute Inc. 1997). These generalized correlations use information on multiple observations per site. The strength of association of contaminant levels with strikes and efficiency was estimated by linear or rank correlation coefficients, with multiple observations per site. The significance of contaminants as covariates of efficiency was modeled by logistic regression, with estimates adjusted for overdispersion from the binomial model. Factor analysis was performed to find combinations of sediment contaminants that would characterize contamination patterns from site to site. Similarly, multiple regression models were developed to explain predation behavior in terms of sets of contaminants. However, these attempts were undermined by extreme values for some contaminants and neither technique produced useful explanatory combinations used in final analyses; thus, the results of these exploratory procedures are not reported. Cluster analyses were performed on the summary indices ΣER-L and ΣER-M and their logarithms. Statistical analyses were performed using Statistix® (Analytical Software, Tallahassee, FL 32317, U.S.A.) and SAS software packages. The overall criterion for statistical significance for data in Tables 2 and 3 was $p < 0.05$; correlations presented as sets of 4–7 contaminants are displayed in Table 4 as significant if $p < 0.01$ (approximate adjustment for experimentwise error using Sedak's method).

Results

Contaminants in sediment

The levels of Hg, Cu, Pb, Zn, and Cd that we measured in the sediments from 11 sites are presented in Table 2. The data from the two Massachusetts sites, ND (Superfund, New Bedford Harbor) and WI (reference, West Island), are taken from published values (Nelson et al. 1996) and do not include standard deviations. The table also includes the Long et al. (1995) ER-L and ER-M values for reference. The levels of contaminants at a site were highly correlated with each other, so that the impact of individual contaminants was confounded, regardless of how the behavioral outcomes were modeled. It can be seen that the sites considered contaminated each have a suite of contaminants. Even some of the sites considered clean (Bullhead Bay, BB and TK) exceed the ER-L values for some metals. The highest value of Hg by far is in BC (Berry's Creek), the Hg-Superfund site. The next highest Hg level is at PC, which is an order of magnitude higher than the remaining sites. The lowest values are at EH (East Hampton), which is an order of magnitude lower than the next group, which includes BB, FC (Foundry Cove), SH (Sandy Hook), UB (Union Beach), and WI. For Cu, the highest sites are BC, NB (Newark Bay), ND, and PC, all generally considered highly contaminated, while the lowest concentrations are at BB, EH, FC, TK, and WI, which, with the exception of FC, are considered the cleanest sites. For Pb, NB is far higher than all the other sites, followed by BC and SH, and the lowest concentrations are at EH, FC, TK, and WI. For Zn, the highest levels are in BC, followed by NB, SC (Scuffletown Creek), and PC, all known to be highly contaminated. The lowest Zn levels are in EH and WI, known clean sites. Cd is highest at BC, followed by ND. The lowest Cd is at WI, followed by EH, SH, and UB. The intermediate levels found at FC reflect the effectiveness of the cleanup at that former Superfund site. It can be seen that for the contaminated sites, many metals are elevated. BC exceeds the ER-M for all five metals. ND and PC exceed the ER-M for two metals, and exceed the ER-L for the other three. Pearson correlations revealed strong correlations among the metals. Hg was correlated with Cd ($r = 0.89$) and with Zn ($r = 0.85$), and Cu was correlated with Pb ($r = 0.75$) and Zn ($r = 0.680$).

Data on organics [total polychlorinated biphenyls (PCB) and total polynuclear aromatic hydrocarbons (PAH) in sediment], taken from other sources (Nelson et al. 1996;

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Table 3. Metal concentrations ($\mu g \cdot g^{-1}$, mean ± standard deviation) in brain and liver, and genetics (frequency of *MdhA-A* – northern allele, taken from Weis et al. 1999) in mummichogs from different sites. See Table 1 for site names.

Site	Cu/Brain	Cu/Liver	Zn/Brain	Zn/Liver	Hg/Brain	Hg/Liver	Pb/Brain	Pb/Liver	*Mdh*
BB	6.79 ± 2.05	137 ± 102	135 ± 24.3	143 ± 26	0.093 ± 0.19	0.692 ± 0.45	3.23 ± 2.54	4.5 ± 8.9	0.93
BC	8.37 ± 0.84	75.8 ± 42.6	193 ± 6.94	142 ± 20.7		1.80 ± 0.69	2.66 ± 2.72	5.8 ± 4.1	0.65
EH	10.5 ± 5.29	264 ± 73.7	183 ± 29.6	183 ± 27.9	0.195 ± 0.16	0.160 ± 0.099	4.11 ± 3.65	6.5 ± 8.3	0.81
FC	3.67 ± 0.21	81.2 ± 49.2	115 ± 6.29	151 ± 46.5	0.212 ± 0.08	0.367 ± 0.12	0.22 ± 0.07	1.1 ± 0.45	0.85
NB	10.9 ± 5.73	325 ± 175	211 ± 64.0	144 ± 32.3	0.244 ± 0.15	0.710 ± 0.32	0.51 ± 0.07	2.7 ± 6.4	0.53
ND	7.42 ± 1.39	183 ± 30.3	158 ± 32.8	72.6 ± 12.6	0.309 ± 0.23	0.147 ± 0.05	9.75 ± 10.34	5.3 ± 3.57	1.0
PC	12.5 ± 5.08	262 ± 125	174 ± 18.5	175 ± 31.6	0.591 ± 0.321	2.92 ± 0.78	13.7 ± 7.83	23.7 ± 28.1	0.67
SC	5.75 ± 1.69	374 ± 135	140 ± 43.1	184 ± 38.3	0.354 ± 0.293	0.421 ± 0.264	2.21 ± 0.26	2.34 ± 0.27	0
SH	11.0 ± 2.64	112 ± 32.1	179 ± 72.8	134 ± 27.8	0.009 ± 0.005	0.033 ± 0.01	2.55 ± 2.62	2.44 ± 5.07	0.54
TK	8.79 ± 1.81	260 ± 126	138 ± 25.7	139 ± 7.10	0.221 ± 0.098	0.515 ± 0.23	0.74 ± 0.21	0.84 ± 0.64	0
UB	9.43 ± 1.84	146 ± 36.4	174 ± 29.0	126 ± 42.3	0.256 ± 0.198	0.127 ± 0.038	11.4 ± 10.2	3.37 ± 2.16	0.6
VL	6.91 ± 2.68	76.8 ± 33.9	165 ± 41.7	117 ± 21.6	0.409 ± 0.076	0.895 ± 0.505	5.40 ± 2.67	2.9 ± 1.53	0.54
WI	5.65 ± 1.96	142 ± 51.3	122 ± 12.7	72.4 ± 17.7	0.186 ± 0.09	0.206 ± 0.09	6.43 ± 6.02	1.2 ± 1.2	1

Table 4. Correlations of behavioral biomarkers with contaminants in sediment and fish tissues and with *Mdh* allele.

Correlate	Adult captures, r_G/p value	Adult strikes, r_G/p value	Efficiency, r_G/p value
Sediment			
Hg	0.01 / 0.96	0.16 / 0.026	–0.07 / 0.29
Pb	–0.34 / 0.002	0.01 / 0.93	–0.22 / 0.0005
Cu	–0.31 / 0.002	–0 / 0.96	–0.17 / 0.009
Zn	–0.13 / 0.13	0.15 / 0.033	–0.14 / 0.027
Cd	–0.21 / 0.044	0.15 / 0.05	–0.18 / 0.009
PCB	–0.29 / 0.016	–0.07 / 0.34	–0.15 / 0.024
PAH	–0.10 / 0.37	0.15 / 0.07	–0.13 / 0.07
Brain			
Hg	–0.18 / 0.08	0.27 / 0.0001	–0.15 / 0.028
Pb	0.16 / 0.12	–0.10 / 0.17	0.08 / 0.21
Cu	–0.02 / 0.88	–0.11 / 0.11	0.07 / 0.30
Zn	–0.25 / 0.010	–0.04 / 0.57	–0.13 / 0.035
Liver			
Hg	0.07 / 0.46	0.12 / 0.09	0.13 / 0.044
Pb	0.05 / 0.58	–0.23 / 0.001	0.20 / 0.002
Cu	0.22 / 0.022	–0.18 / 0.009	0.17 / 0.008
Zn	0.36 / 0.0002	–0.04 / 0.58	0.29 / 0.0001
Mdh	–0.27 / 0.001	–0.19 / 0.008	0.02 / 0.73

Note: r = linear correlation coefficient; r_G = generalized correlation coefficient for discrete data. Data are underlined when $p \leq 0.01$.

Eckenfelder Inc. 1991; Adams et al. 1998), are also shown in Table 2. The sites considered clean did not exceed ER-L values for these organic contaminants except for PCBs at WI. On the other hand, BC, FC, NB, ND, PC, SH, and UB exceed the ER-M for PCBs. This reflects the general contamination in the N.Y./N.J. Harbor Estuary and Hudson River, as well as the Superfund site in New Bedford (ND), which had PCB levels that were an order of magnitude higher than all other sites. The only site that exceeded the ER-M for PAH was SC, across the Elizabeth River from the Atlantic Wood Superfund site. NB, PC, and VL (Vince Lombardi Rest Stop) also had quite high levels.

Contaminants in fish tissue

Concentrations of metals in brain and liver of fish from the different sites are displayed in Table 3. Although we started to do Cd analyses, there was never much accumulation, so we ceased this analysis. A number of trends can be seen.

For Cu, the highest liver values are for NB and SC, two highly polluted sites. The brain levels tend to be two orders of magnitude lower than liver concentrations and do not vary greatly among sites. NB is the among the highest for brain Cu also, although SC has rather low levels, and EH and SH also have high levels. The lowest liver levels are at VL, FC, and BC. FC also has the lowest brain Cu. Thus, while BC and ND have among the highest sediment levels of Cu, the liver and brain levels are not correspondingly high, and while EH has among the lowest levels in the sediments, tissue levels are not correspondingly low. Correlations revealed low associations between Cu in sediments and liver ($r = 0.37$), between sediments and brain ($r = 0.45$) and between liver and brain ($r = 0.33$).

For Zn, the liver levels did not vary greatly, and ranged from around 70 (WI and ND, the two Massachusetts sites) to about 180 (EH and SC): these two lowest and two highest values each include a Superfund site and a reference site. Unlike Cu, the brain levels of Zn were quite similar to the liver levels and also did not vary greatly among sites. Correlations between Zn in sediments and the liver were low ($r = 0.21$), between sediments and brain were moderate ($r = 0.54$), and between brain and liver were low ($r = 0.21$).

For Hg, PC and BC stand out as having the highest liver levels, about an order of magnitude higher than the other populations. These sites are the most Hg contaminated. The sites with the lowest Hg in the liver are EH, ND, SH, and UB. Brain Hg was lowest in BB, EH, and WI, the three cleanest sites, and highest in PC and VL. [It is unfortunate that we do not have data on Hg in brains of BC fish, since this is the most highly Hg-contaminated site. Fish were difficult to obtain at this site, and those obtained were rather small. Brains from many fish had to be pooled to obtain enough mass for analysis, and since Hg is analyzed separately from the other metals, the analysis could not be done.] Correlations were found for Hg between sediment and liver ($r_S = 0.68$) and sediment and brain ($r_S = 0.55$), while correlations between liver and brain were low ($r_S = 0.17$).

For Pb in the liver, the highest concentrations were in PC fish, followed by BC, EH, ND, and BB. It was surprising to find high liver Pb in BB and particularly in EH, one of two

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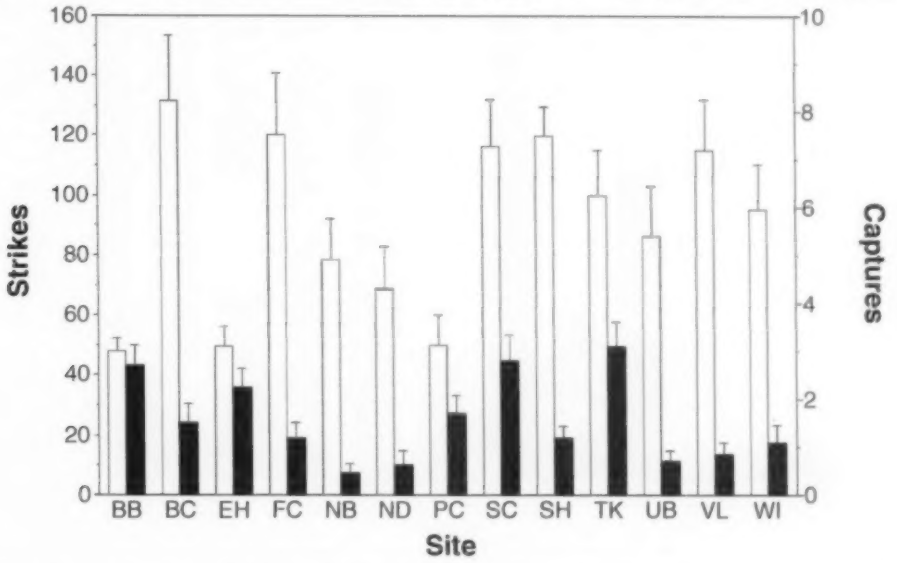
Fig. 1. Average number of strikes and captures (± standard error of mean) of grass shrimp in 30 min by adult mummichogs of the different populations. BB = Bullhead Bay, N.Y.; BC = Berry's Creek, N.J.; EH = East Hampton, N.Y.; FC = Foundry Cove, N.Y.; NB = Newark Bay, N.J.; ND = New Bedford Harbor, Mass.; PC = Piles Creek, N.J.; SC = Scuffletown Creek, Va.; SH = Sandy Hook, N.J.; TK = Tuckerton, N.J.; UB = Union Beach, N.J.; VL = Vince Lombardi Rest Stop, N.J.; WI = West Island, Mass. □, Strikes; ■, captures.



sites in which the sediment levels are below the ER-L. The lowest liver concentrations were found in TK, WI, and FC. Brain Pb was highest in PC and UB, and lowest at FC, NB, and TK. Low and (or) inverse correlations were seen among the Pb levels in the different compartments: sediment and brain ($r = -0.39$), sediment and liver ($r = -0.12$), and brain and liver ($r = 0.40$).

Thus, Hg was the only metal in which correlations were generally seen between levels in sediments and tissues.

Prey captures

The numbers of captures and strikes made by the fish are shown in Fig. 1. The populations with the highest number of captures include TK, EH, and BB, three of the cleanest sites. Those with the lowest capture rates are NB, ND, UB, and VL, three of which are located in the generally contaminated northern N.J. area and one of which is near the New Bedford, Mass., PCB Superfund site. It is interesting, however, that fish from some of the most highly polluted sites (SC, BC, and PC) are not among the groups with the lowest capture rates. The number of captures at all sites was highly variable. Consequently, effects are detectable only as broad patterns observed in the mean or aggregate. Adjustment for overdispersion provides only approximate p-values.

ANOVA for the 13 populations showed highly significant differences ($F = 5.76$, $p < 0.0001$); pairwise comparisons indicated captures at BB, SC, and TK were significantly greater than those at VL, UB, ND, and NB. NB also had fewer captures than EH. All other groups were intermediate.

The number of strikes also varied considerably, ranging from ~50 strikes (made by the three fish in 30 min) for BB, EH, and PC, to about 120 strikes by BC, FC, SC, SH, and VL, as seen in Fig. 1. ANOVA for strikes was highly significant ($F = 4.03$, $P < 0.0001$). Pairwise comparisons indicated that BC, FC, SH, and VL had significantly higher numbers of strikes than EH and BB. All other groups were intermediate. Thus, the number of strikes did not relate to the number of captures, since some groups with the highest number of strikes had the lowest captures. Thus, efficiency was different for the different populations. The highest efficiencies of 5.9%, 4%, 3.4%, and 2.9% were seen in BB, EH, PC, and SC, respectively (most of which have high capture rates), while the lowest efficiencies of 0.3%, 0.5%, 0.6%, and 0.9% were seen in NB, UB, VL, and ND, respectively; groups with the low capture rates. Thus, there are contaminated populations with both high (PC, SC) and low (NB, ND) efficiencies. The very low efficiency overall reflects the difficulty of capturing grass shrimp, a species with very effective predator avoidance capabilities (Smith and Weis 1997). ANOVA with pairwise comparisons showed that efficiency at BB and EH was significantly higher than at any of ND, NB, WI, BC, UB, SH, FC, and VL. BB also had higher efficiency than TK, and PC was higher than VL.

Gut contents

The gut contents of fish from 10 of the populations (missing ND, WI, and SC) are expressed as percentage detritus, percentage shrimp, and percentage "other" (Fig. 2). The "other" category in the various populations consisted of other crustaceans, insects, worms, small fish, and unidentifiable material. The highest amounts of detritus were found in the fish from PC, FC, and BC, all of which had detritus making up >50% of their gut contents. The lowest amounts of detritus were in BB (1%) and UB (14%). Grass shrimp made up the largest proportion of the diet of fish from BB (64%), EH (45%), and TK (25%), which are among the cleanest sites and among the sites with the highest capture rates. (We did not analyze gut contents in fish from the

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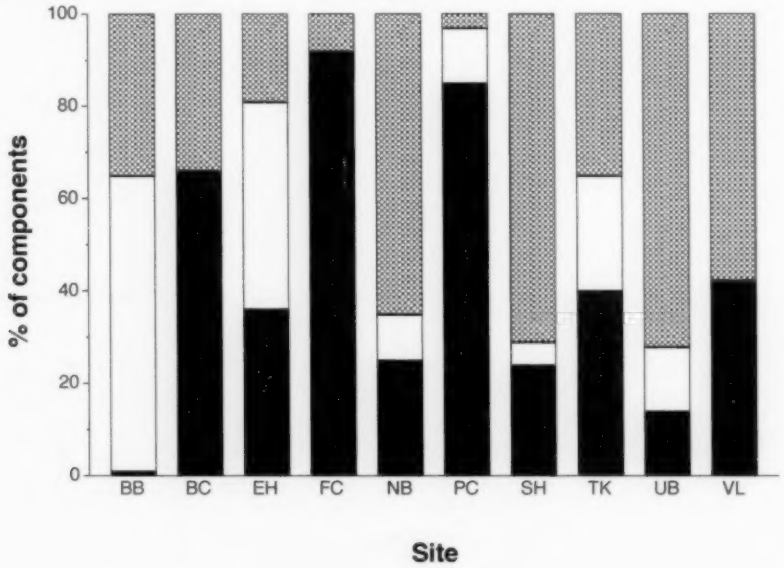
Fig. 2. Gut contents of adult mummichogs from the different populations. BB = Bullhead Bay, N.Y.; BC = Berry's Creek, N.J.; EH = East Hampton, N.Y.; FC = Foundry Cove, N.Y.; NB = Newark Bay, N.J.; ND = New Bedford Harbor, Mass.; PC = Piles Creek, N.J.; SC = Scuffletown Creek, Va.; SH = Sandy Hook, N.J.; TK = Tuckerton, N.J.; UB = Union Beach, N.J.; VL = Vince Lombardi Rest Stop, N.J.; WI = West Island, Mass. ■, % detritus; □, % shrimp; hatched bars, % other.



fourth high capture site, SC.) Shrimp were absent from the diet of fish from BC. We have not observed shrimp at BC, so the absence in the diet may reflect an absence of shrimp. In contrast, FC, VL, NB, and PC, which also have no or low amounts of shrimp in diets (0%, 0.2%, 10%, and 12%, respectively), have abundant, i.e., easily collected, populations of *P. pugio*. Furthermore, the shrimp were found to be three times more numerous at PC than at TK (Santiago Bass et al. in press), while the gut contents had more than twice as much shrimp in TK fish (25%) than in PC fish (12%). Thus, shrimp in gut contents was not consistent with shrimp availability, but was consistent with fish predatory ability. BC was the only site in which several fish had empty guts.

Relationships between contaminant levels and behavior

A number of Poisson and logistic regressions were performed to investigate the association between levels of the various contaminants and aspects of behavior. Many of these were statistically significant, but a great degree of scatter in the data within each site and high deviance from the model indicated a weak fit. Generally, significant correlations were seen with many individual contaminants in sediments and in fish tissues (shown in Table 4). Since many of the contaminants co-vary, the responses may reflect overall contaminant loading, rather than responses to individual metals.

As shown in Table 4, the strongest correlations with captures were sediment Pb, Cu, and liver Zn, this last one being a positive rather than negative correlation. The strongest correlation with strikes was brain Hg, and with efficiency was liver Zn. PAH in sediment was positively but not strongly associated with strikes ($r = 0.15$). The lack of negative effect of PAH on behavior was clear with the SC fish from near the Atlantic Wood creosote Superfund site, which had the highest PAH levels. Although these fish were dying in the laboratory, they remained active predators until the end, achieving the second highest capture rate.

The summed (Σ) ER-L and ER-M equivalents for each site are shown in Appendix 1. These equivalents, which may be considered a general index of contamination, were used to divide the populations into three groups: (1) ΣER-L equivalent below 10, ΣER-M equivalent below 2: BB, EH, and TK; (2) ΣER-L equivalent 20–40, ΣER-M equivalent 3–6: FC, SC, SH, UB, VL, and WI; and (3) ΣER-L equivalent over 50, ΣER-M equivalent over 10: BC, NB, ND, and PC. This grouping was consistent with cluster analysis based on the logarithm of those two summary indices. The average number of captures per site was significantly higher in the least contaminated sites than among the other two groups with a mean of 2.68 vs. 1.31 and 1.08 (ANOVA, $p < 0.0001$). Efficiency was significantly higher as well: 4.33% vs. 1.22% and 1.45 % (ANOVA, $p < 0.0001$). When the sites' capture ranks are plotted against the degree of contamination (ΣER-M), the generally inverse relationship, although not significant, can be appreciated (Fig. 3).

Relations of genetics with behavior

There was a statistically significant relationship between the *Mdh-A(a)* allele and captures, with relatively more captures seen in the southern populations. The generalized correlation coefficient (r_G) for *Mdh* and captures was –0.27. At the two geographical extremes, the clean northern WI population in Massachusetts had a low prey capture rate, while the southern PAH- and metal-contaminated SC population in Virginia had a very high capture rate. Strikes were also

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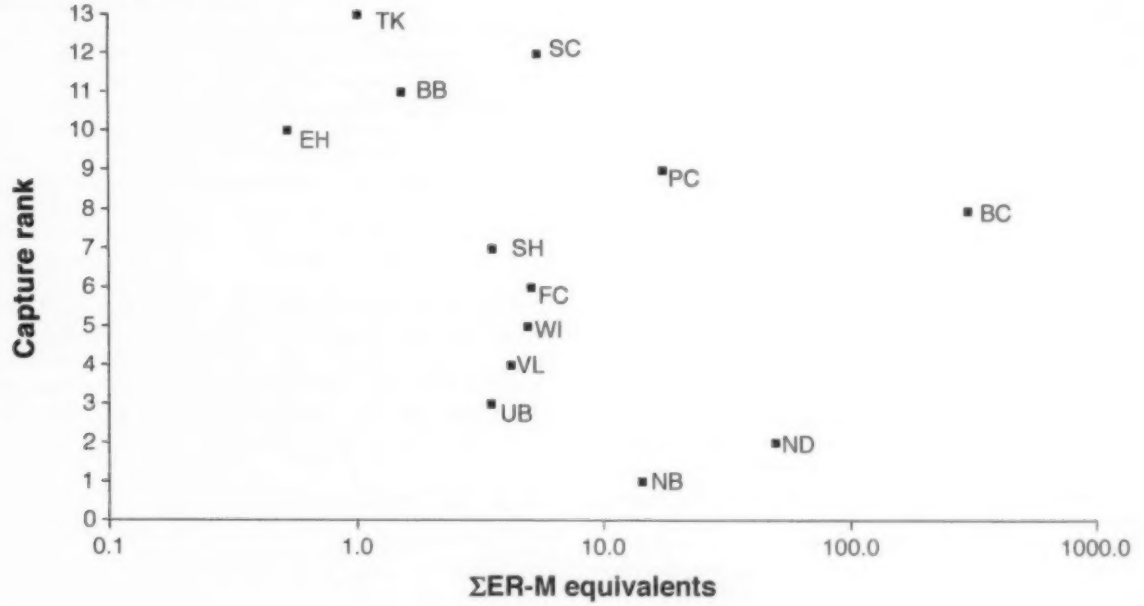
Fig. 3. Correlation of captures with overall contamination. Sites, arranged by rank for captures are plotted against the total (Σ) ER-M equivalents, indicators of overall levels of contamination. BB = Bullhead Bay, N.Y.; BC = Berry's Creek, N.J.; EH = East Hampton, N.Y.; FC = Foundry Cove, N.Y.; NB = Newark Bay, N.J.; ND = New Bedford Harbor, Mass.; PC = Piles Creek, N.J.; SC = Scuffletown Creek, Va.; SH = Sandy Hook, N.J.; TK = Tuckerton, N.J.; UB = Union Beach, N.J.; VL = Vince Lombardi Rest Stop, N.J.; WI = West Island, Mass.



higher in the southern population (r = –0.19, p = 0.01). These modest but significant correlations also represent a great degree of spread in the data.

Associations of gut contents with behavioral parameters

There was a strong correlation between the amount of grass shrimp in the guts of field-collected fish and the captures of shrimp in the laboratory ($p < 0.0001$). This relationship indicates that the populations that captured shrimp well in the lab also do so in the field, and supports the validity of laboratory studies on prey capture as ecologically realistic. This can be considered a field validation of this behavioral measure.

Discussion

The overall behavioral responses observed in the fish were generally consistent with the distribution and concentration of contaminants, indicating that prey capture may be a possible behavioral biomarker for environmental contamination. However, only weak correlations between specific pollutants and behavior were found (very high deviance seen in all "statistically significant" correlations). The best fitting models, with four or five covariates, explained less than 15% of the variability. Adding and dropping variables revealed that the models and even the direction of the slope were very sensitive to small changes, again a consequence of confounding. High variability and confounding are common in field studies. The three cleanest populations, TK, EH, and BB, had the highest capture rates in the lab and the greatest amount of shrimp in their gut contents. The most contaminated sites, NB, BC, ND, and PC had lower captures, although BC and PC did not have as low capture rates as might be expected. SC had higher captures than might be expected. WI, UB, and VL had lower capture rates than might be predicted from their contaminant levels. However, UB and VL exceeded the ER-L for most contaminants, while WI did not exceed it for any contaminant except for PCBs.

A possible explanation for the higher-than-expected performance of the PC and BC fish could be that these populations have adapted and have become more resistant to the contaminants at their sites. We have previously noted elevated tolerance to Hg in gametes and embryos in the PC population, allowing embryos to be unaffected when exposed to concentrations of methylmercury that cause embryological malformations in reference populations. We did not see tolerance to acute effects of methylmercury in juveniles or adults, however (Weis and Weis 1989). Nevertheless, it is not unreasonable to think that adults could have developed some tolerance to the suite of toxicants in terms of their behavioral responses. Studies done on the Elizabeth River Atlantic Wood site (across from SC) fish demonstrate that these fish are also very tolerant to the hydrocarbons in their environment (Armknecht et al. 1998), which may explain the higher-than-expected performance by SC fish. Resistance of ND mummichogs to the high level of PCBs in their environment has also been demonstrated (Nacci et al. 1999); nevertheless, they are among the groups with the lowest prey capture. However, the performance of the WI clean reference fish is also poor. This may reflect geographic

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genetic differences between the northern and southern subspecies. Black et al. (1998) noted that PCB-treated fish had reduced food intake, which may be related to our observations on the ND fish.

Another reported phenomenon in populations from contaminated sites is that they tend to accumulate proportionately lower amounts in relation to sediment levels than populations from cleaner sites. This may be due to greater excretion or reduced uptake (Khan et al. 1989). This has been reported in mummichogs (Chernoff and Dooley 1979; Khan and Weis 1993).

The ER-L and ER-M values (Long et al. 1995) reflect sediment contaminant levels that are likely to cause adverse effects. Their accuracy as predictors of effects has been tested primarily in laboratory toxicity tests with benthic organisms. Mummichogs are affected indirectly (primarily via food), rather than directly by sediment contaminants, and are generally more tolerant than the benthic species (e.g., amphipods) used in sediment toxicity tests. Nevertheless, significant deficits in prey capture behavior were seen at all the severely degraded sites and at some of the intermediate sites. The data reflected the general contamination in the N.Y./N.J. harbor area, as did toxicity tests with amphipods (Long 2000). Significant correlations were seen for many individual contaminants in sediments and in fish tissue. Since many of them co-vary, the responses reflect overall contamination rather than responses to individual chemicals. The data do seem to indicate, however, that PAH does not cause this behavioral response.

These correlations of behavior with contaminant levels, though statistically significant, are not convincing because of the great amount of spread in the data. Indeed, some of the relationships go the "wrong" way, i.e., positive correlations were found rather than the expected negative correlation with concentration. The statistical significance is largely a product of the high *N*.

The great variability of associations between tissue levels and behavior supports others' conclusions that bioaccumulation does not reliably predict biological effects (Chapman et al. 1998). Mercury was the only contaminant in which the liver and brain levels were significantly correlated with sediment levels. This is in keeping with the findings of Wren et al. (1983), who studied uptake of 21 elements and found that only Hg bioconcentrated in fish. Organisms can maintain internal concentrations of essential metals (Cu and Zn) via homeostatic mechanisms; therefore, there would be no relation between exposure to these metals and bioconcentration (Chapman et al. 1998). Reduced bioaccumulation in more contaminated sites may contribute to the lack of consistency in the liver and brain values vis-à-vis behavior.

When the three groups of populations (by summed ER-L and ER-M equivalents) are considered, it can be seen that the cleanest sites, group 1, are those with the highest prey capture rates. Of those populations with the highest contamination, group 3, NB and ND have very low capture rates (<1), and PC and BC have intermediate capture rates (1–2). Of the populations in the intermediate group, FC, SH, and WI have intermediate capture rates (1–2), while SC (at 2.8) is higher than would be predicted, and UB and VL (<1) are lower than predicted. Tolerance may partially explain why SC, PC, and BC have higher prey capture than would be predicted. Also, a major contaminant at SC is PAH, which is probably not associated with the behavioral deficit. Why UB and VL fish, with intermediate genotype and intermediate contamination have such low capture rates, we do not know. UB sediment is rather sandy, which might make contaminants more bioavailable. There may be other contaminants or other environmental factors that contribute to poor performance. The contamination pattern and levels may not be high enough to trigger development of tolerance. Another possibility in these sites, which have been improving in environmental quality, is that the behavioral responses to the improving conditions may happen over a different time scale (Depledge 1999). As an ecosystem recovers from stress, the rate and extent of recovery may differ for different responses. The rates and lag times for recovery for particular responses have not yet been determined.

As part of the EMAP program, some bioindicators were evaluated to see how well they correlated with estuarine conditions (Summers et al. 1997). They focused at both ends of the spectrum, i.e., at reference sites and at heavily impacted sites, and found that certain of these indicators (pathologies, splenic macrophage aggregates, and vertebral abnormalities) showed promise. If we remove our intermediate sites, and just include sites in group 1 (reference) and 3 (heavily impacted), more significant associations would be seen. Using only those sites, the correlations of captures increase dramatically with sediment Hg ($p = 0.01$), sediment Cu ($p < 0.0001$), sediment Pb ($p < 0.0001$), sediment Zn ($p = 0.0002$), and sediment PCB ($p < 0.0001$).

A number of studies have measured various indicators in field populations and tried to associate the biomarkers with levels of various contaminants. Chang et al. (1998) studied liver lesions in winter flounder (*Pleuronectes americanus*) in northeast U.S. estuaries and found associations between certain lesions and low-molecular-weight PAHs, certain pesticides and metals, but not dichlorodiphenyltrichloroethane (DDT). Other lesions were associated with PAHs, other pesticides, Ag, Cu, and Sn, but not PCBs. A third type of lesion was associated with PCBs, As, Zn, Ni, and Hg but not PAHs and DDT.

Ringwood et al. (1999) examined cellular responses (lysosomal destabilization and glutathione production) in oysters deployed at 15 sites and found significant correlations between the responses and metals, but since the metals covaried, the responses were to overall loading rather than to particular metals. Similarly, in our study, responses could not be definitively linked with specific contaminants due to covariance but appear to be more general responses to overall contamination.

Prey capture as a behavioral biomarker is ecologically relevant and corresponds well to fish diet in the field. However, it does not appear to be especially sensitive due to the great variability in behavior among the fish from each site. Leamon et al. (2000) evaluated four health indices in mummichogs from five uncontaminated sites and also found great variability in mean values. It was not clear whether differences in microhabitat, resource partitioning, or other factors were responsible for the variation. They concluded that health index studies in such an inherently variable species may be meaningless outside a given population. The behavioral differences in our study did seem to be related to over-

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all contaminant levels rather than to a specific toxicant, and the development of tolerance in some highly contaminated populations can obscure results.

Acknowledgments

We thank Ted Proctor, Frank Kemp, Celine Santiago Bass, John Hogan, and Esther Hager for technical assistance, and Tim Gleason, Nicolay Mugue, and Michael Newman for providing samples from distant sites. This work was supported by a grant from the USGS Division of Water Resources Research, No. 1434HQ-96-JR-02686.

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Appendix. Summed ER-L (ΣER-L) and ER-M (ΣER-M) equivalents at each site, ranked by degree of contamination (ΣER-M) values), and grouped in low (1), intermediate (2), and high (3) levels of contaminants. See Table 1 for site names and descriptions.

Site	ΣER-L	ΣER-M	Grouping
EH	2.95	0.53	1
TK	7.24	1.02	1
BB	7.84	1.54	1
UB	22.36	3.53	2
SH	21.68	3.56	2
VL	25.47	4.21	2
WI	38.02	4.98	2
FC	37.21	5.11	2
SC	34.33	5.48	2
NB	88.01	14.44	3
PC	103.6	17.52	3
ND	386.9	50.31	3
BC	1450	302.8	3

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Empirical relationships between watershed characteristics and coho salmon (*Oncorhynchus kisutch*) smolt abundance in 14 western Washington streams

Rishi Sharma and Ray Hilborn

Abstract: We assembled data on coho salmon (*Oncorhynchus kisutch*) from 14 streams in western Washington, including annual smolt counts and annual escapement, either as absolute counts or as an index. We also compiled data on large woody debris (number·km^{-1} of stream), road densities in the watersheds (km road·km^{-2}), gradient of the streams (%), valley slope adjacent to the stream (%), drainage area in the watershed (km^2), and pool, pond, and lake areas (m^2·km^{-1}). We explored the relationships between habitat variables and two measures of coho production, the maximum production of smolts in the stream (capacity) and the maximum smolts/spawner (productivity). Using the 11 streams with pool and pond counts, we found that pool and pond densities served as good predictors of smolt density (r^2 = 0.85 for pools and 0.68 for ponds, independently). Pools produced 0.39 smolts·m^{-2} and ponds produced 0.07 smolts·m^{-2} in the multiple regression fit, accounting for 92% of the residual error. We also found that lower valley slopes, lower road densities, and lower stream gradients were correlated with higher smolt density.

Résumé : Nous avons rassemblé des données sur le Saumon coho (*Oncorhynchus kisutch*) de 14 cours d'eau du Washington occidental, entre autres des recensements annuels de saumoneaux et des échappées annuelles, tant en valeurs absolues qu'en indices relatifs. Nous avons aussi compilé des informations sur la présence de débris ligneux de grande taille (nombre·km^{-1} de cours d'eau), sur la densité des routes dans le bassin versant (km route·km^{-2}), la pente du cours d'eau (%), la pente de la vallée adjacente au cours d'eau (%), la surface de drainage dans le bassin versant (km^2), ainsi que la surface des profonds, des étangs et des lacs (m^2·km^{-1}). Nous avons alors exploré la relation entre les variables de l'habitat et deux mesures de production des saumons, la production maximale de saumoneaux dans le cours d'eau (capacité) et le maximum de saumoneaux par géniteur (productivité). Dans les 11 cours d'eau pour lesquels nous avions des données sur les profonds et les étangs, les densités des profonds et des étangs se sont avérées être de bonnes variables prédictives de la densité des saumoneaux (r^2 = 0,85 pour les profonds et 0,68 pour les étangs, indépendamment). Une régression multiple qui explique 92% de l'erreur résiduelle indique que les profonds produisent 0,39 saumoneau·m^{-2} et les étangs 0,07 saumoneau·m^{-2}. Les valeurs plus faibles de pentes des vallées, de densités des routes et de pentes des cours d'eau sont liées aux densités de saumoneaux plus élevées.

[Traduit par la Rédaction]

Introduction

The decline in salmon in the Pacific Northwest is ascribed to a combination of factors including habitat loss and degradation, overharvesting, hatchery practices, and changes in marine conditions (NRC 1996; Weitkamp et al. 1995; Bisson et al. 1997). As society seeks to rebuild these populations, we must make choices among alternative efforts in reducing harvesting, changing hatchery practice, and modifying or preserving habitat. Without quantitative relationships describing the impact of these factors on salmon production, such choices cannot be made rationally. Despite the vast amount of work on the impact of habitat on salmonids, there are surprisingly few relationships established between easily measurable habitat variables and the ability of habitat to produce salmon on a watershed scale. Moreover, there have been few attempts to link land uses to changes in habitat or salmon production.

Bradford et al. (1997) assembled data on 106 coho salmon (*Oncorhynchus kisutsch*) streams where smolt counts were available (through mark–recapture methods). The habitat variables assembled in their database were stream length, watershed area, stream gradient, valley slope, and geographical latitude. However, the only habitat variables that explained variation in smolt production were stream length and geographic latitude. Nickelson et al. (1992*a*, 1992*b*) described empirical relationships for 18 Oregon streams between different habitat types and the density of overwintering juvenile coho found in those habitats. Their work suggests that pool and pond areas should be good predictors of smolt production in coho systems as they provide

Received October 23, 2000. Accepted May 17, 2001.
Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 21, 2001.
J16030

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 DOI: 10.1139/cjfas-58-7-1453 © 2001 NRC Canada

Table 1. Smolt trap counts.

Location	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
Bear Creek				571	604	439	508	816	801	251
Courtney Creek				1 147	1 130	1 034	1 436	1 165	1 507	1 039
Lost Creek					3 633	1 936	4 743	1 587	3 026	1 949
Wildcat Creek					5 941	2 158	4 193	3 763	5 540	2 964
Snow Creek				5 201	9 156	9 090	8 344	7 048	7 700	1 871
Little Tahuya Creek				5 560	9 772	3 748	9 042	9 615	7 278	10 228
Mission Creek							19 023	15 218	18 716	17 011
Mill Creek		33 020	23 241	15 788	22 191	9 036	20 138	24 103	33 048	35 088
Big Beef Creek	20 374	39 954	37 054	18 600	47 300	20 755	40 076	24 596	26 724	36 646
Little Pilchuk Creek	22 640	35 588	35 846	32 575	13 009	22 397	36 292	26 680	25 739	24 098
Bingham Creek								31 806	33 464	43 945
Harris Creek					23 632	11 824	30 035	34 951	17 062	29 025
Deschutes River					60 275	65 776	131 261	64 757	65 518	101 901
S.F. Skykomish River			291 991	358 104	281 624	298 736	215 788	228 603	226 633	191 692

Note: Data as per Chuck Baranski (1989, Washington Department of Fish and Wildlife, 600 Capitol Way N, Olympia, WA 98501-1051) and Mindy

a buffer in the overwintering of the juvenile coho salmon and are therefore causally related to smolt abundance in a stream. Other studies have also simply measured the abundance of juvenile fish per unit area of different types of habitat (Quinn and Peterson 1996; Holtby and Scrivener 1989; Chapman 1966) but not the actual production of juveniles as measured by downstream migration.

Some studies have also been done on reach-specific sites to estimate smolt outmigrants. Letselle et al. (1996) and Reeves et al. (1989) suggest reach-specific characteristics to estimate overall smolt production. The limiting factors analysis and the EDT (ecosystem diagnosis and treatment) approach both use reach-specific habitat characteristics by life stage of juvenile salmon to determine smolt abundance for a stream. Beechie et al. (1994) tested the Reeves et al. (1989) methodology on the Skagit River in western Washington and found it to be reasonably accurate on different levels of resolution (both reach-specific and river-basin-specific). However, on a watershed level, few studies have tried analyzing what may be the important habitat variables that relate to smolt abundance, and a more simplified data-driven approach is examined in this paper. The cross-sectional analysis across different streams in a watershed examined here could help in understanding the common variables that correlate to smolt abundance and in determining the important stream characteristics related to higher abundance in large watersheds.

Other studies have shown how systems change in relation to human impacts. Jones and Grant (1996) showed that long-term changes have occurred in stream flows associated with clearcutting and road construction. Jones and Grant (1996) demonstrated that peak discharges increased in some streams because of changes both in flow routing as a result of road construction and in water balance as a result of clearcutting and forest succession. Tripp and Poulin (1986) and Quinn and Peterson (1994) have shown a decrease in egg–fry survival because of increased peak flows. In addition, Everest et al. (1987) points out that sedimentation caused by erosion and landslides (indirectly linked to road density) is also a major cause of reduction in freshwater habitats essential for juvenile salmon. Urbanization also leads to increased road density as well as loss of habitat resulting from ditching, diking, and draining (Sherwood et al. 1990; Beechie et al. 1994). Road density is the only land-use variable related to smolt abundance in our analysis and may serve as an indicator of these effects.

The purpose of this study is to combine the approachs of Bradford et al. (1997) and Nickelson et al. (1992*a*, 1992*b*); we will explore systems for which total smolt counts are available and relate the smolt abundance to habitat and watershed variables. This paper explores simpler habitat–smolt relationships so that predictions can be made at a regional scale provided that sufficient spawners come back to a particular system. This would provide a quantitative measure to evaluate stream habitat modifications and their consequence on overall smolt abundance on a regional scale. The end products of our analysis are quantitative relationships between different stream habitat characteristics, different watershed characteristics, and smolt abundance and the uncertainties surrounding these estimates.

Materials and methods

Smolt and adult data

We assembled data on available smolt counts from different streams across Washington State. Study streams had long time-series of annual smolt counts, normally via weirs or scoop traps. Stream locations are shown in Fig. 1.

All smolts are progeny of spawners two years previously (Table 1). For some streams, an estimate of total female spawners was available (Table 2), usually from counts of redds (the observed redds in surveyed areas are expanded to the entire system based on expansion factors for the particular system), whereas on other streams, only peak index counts of the number of fish per mile were available.

Stream- and watershed-specific variables

The independent variables used in this analysis were organized into three specific categories: (*i*) stream-specific attributes such as pool areas, pond areas, woody debris, stream length, and stream gradient, (*ii*) watershed-specific variables (drainage area and valley slope), and (*iii*) land-use variables for which road density serves as an index.

The three categories are not mutually exclusive. The stream attributes are often related to the watershed and land-use variables. However, this categorization may suggest some likely independent

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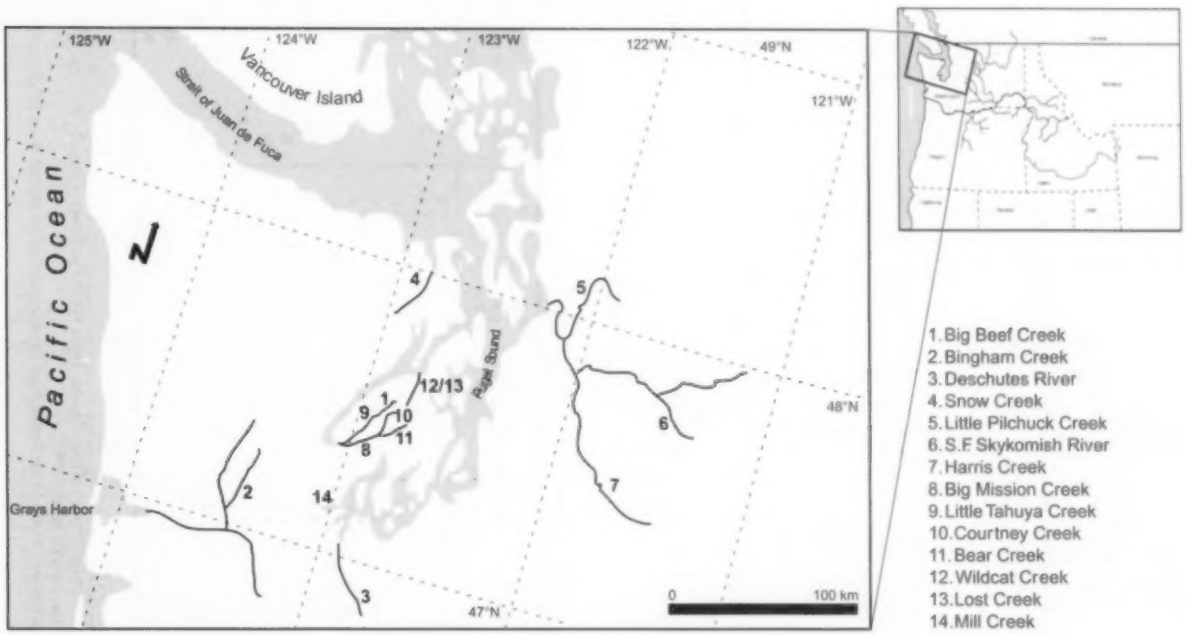
1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
755	667	112	636	992			538	413	138
1 451	1 415	238	1 483	1 460			1 755	1 234	1 041
2 496	1 213								
5 317	3 598								
6 947	10 113	641	6 296	6 915	448	4 300	4 787		
11 027	4 448	1 357	2 735	7 761			5 943	3 873	3 117
15 770	7 318	7 091	14 528	13 906			18 261	13 010	15 548
33 920	21 175	26 902	18 418	28 230					
25 446	23 637	10 872	24 614	16 437	19 427	22 563	18 720	13 071	18 431
24 916	34 808	33 373	36 723	20 467					
30 939	25 205	22 233	15 742	29 041	23 712	27 639			
35 039	25 970	24 289	26 218	22 773					
64 452	99 241	91 057	54 397	117 087	133 066	11 248	57 204		
184 584									

Rowse, Point No Point Treaty Council, 7999 NE Salish Lane, Kingston, WA 98346, fide Lestelle et al. 1993.

Fig. 1. Map of western Washington, U.S.A., showing the respective study sites.



predictors to relate to the abundance of coho smolts by system (basin-wide approach).

Table 3 shows the various stream attributes. Most of the stream-specific variables (gradient, valley slope, drainage area, and stream length) used in the analyses were obtained from Bradford et al. (1997). Specific stream characteristics such as woody debris and pool, pond, and lake areas were obtained from Baranski (1989) and from independent surveys conducted by the Point No Point Treaty Council (Mindy Rowse, Point No Point Treaty Council, 7999 NE Salish Lane, Kingston, WA 98346, personal communication).

Road density was obtained from a geographic information system database (Lunetta et al. 1997) at a Washington area unit (WAU) scale. This scale is typically 40–200 km^2 in resolution and encompasses areas larger than some of the stream watersheds analyzed here. Because the resolution of these WAUs is extremely large, we actually overlap multiple watersheds in our stream database, and hence the same road density is used for some of the streams in this analysis. The purpose of analyzing this relationship was to determine if any surrogate measure for land use (road density serves as an index for intensity of land use) could be related to smolt abundance on a watershed level.

Spawner–recruit analysis

Where we had both spawner and smolt counts, we fit the data to a spawner–recruit model incorporating habitat constraints (described by Moussali and Hilborn (1986)):

$$(1) \qquad S_t = \frac{E_{t-2}}{\frac{1}{p} + \frac{1}{c} E_{t-2}}$$

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Table 2. Escapement data.

Location	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
Female escapement counts																	
Snow Creek	187	522	288	166	328			253	179	22	240	340	7	49	56		
Big Beef Creek	1018	654	295	1 108	499	411	465	277	883	227	1053	514	283	368	188	283	517
Bingham Creek					355	1268	946	543	2869	914	1445	963	5895	1905			
Deschutes River		2784	905	3 104	1 135	1599	3669	1946	1871	2609	2069	5185	3188	473	1340		
S.F. Skykomish River	6000	9000	9887	14 671	12 389	7725	3255	2688	1747								
Peak index counts																	
Bear Creek		1.8	22	20	56	26	6	2	32	24	14	48	6	36	14	20	
Courtney Creek		7.3	71.3	30	23.9	15	12.5	6.2	10	13.8	30	35	3.8	25	7.5	7.5	
Little Tahuya Creek		33	103	30	112	24	176	11	48	29	95	110	10	27	12	51	
Mission Creek	11.9	60	27.3	12.5	186.7	12.1	23	23.9	80	30.5	53.3	40	5.8	23.2	20.5	16.8	

Note: Data as per Bill Tweit, Washington Department of Fish and Wildlife, 600 Capitol Way N, Olympia, WA 98501-1051, fide Lestelle et al. 1993).

Table 3. Stream specific habitat attributes, watershed attributes, and road density.

Names	Length (km)[a]	Drainage area (km^2)[a]	Gradient (%)	Valley slope (%)	Pool area (m^2)[b]	Total area (m^2)[b]	Pool length (m)[b]	Pond area (m^2)[b]	Lake length (m)[b]	Lake area (m^2)[b]	Road density ($km \cdot km^{-2}$)[c]	Actual count (LWD)[d]	Proportion sampled	LWD count extrapolated
Bear Creek	2.36	31.2	0.03	0.22	2 511	5 593	0	0	0	0	2.58	na	na	na
Courtney Creek	4	13	0	0	5 959	10 866	0	0	0	0	3	467	0.39	1 197
Lost Creek	3	19	0	0	5 125	9 178	0	0	0	0	3	na	na	na
Wildcat Creek	6.72	27.5	0.02	0.29	10 189	18 248	0	0	0	0	2.83	na	na	na
Snow Creek	8.8	30.8	0.027	0.25	21 227	56 806	0	0	750	24 000	2.44	573	1	573
Little Tahuya Creek	1.39	0.87	0.02	0.09	9 788	12 038	2 030	28 103	0	0	2.58	304	0.48	629
Mission Creek	15.15	75.1	0.01	0.18	36 727	74 812	0	0	0	0	2.58	887	0.49	1 810
Mill Creek	16.51	184	0.003	0.09	78 618	118 118	2 150	38 640	2 100	838 072	2.86	na	na	na
Big Beef Creek	16.4	35.7	0.01	0.25	45 920	71 165	3 028	23 178	953	776 710	2.83	624	0.175	3 570
Little Pilchuk Creek	9.74	79.3	0.01	0.03	26 414	28 726	7 789	312 892	610	30 500	2.3	na	na	na
Bingham Creek	22.2	90.7	0.01	0.13	na	na	na	na	na	na	2.68	na	na	na
Harris Creek	11.61	80.3	0.01	0.11	27 486	37 007	2 355	102 057	0	0	2.2	na	na	na
Deschutes River	54	414	0.003	0.1	na	na	na	na	na	na	3.9	2 119	0.22	9 455
S.F. Skykomish River	92.4	932	0.009	0.127	na	na	na	na	na	na	0.48	na	na	na

Note: na, not available.

[a]Bradford et al. (1997).

[b]Baranski (1989), fide Lestelle et al. (1993), Point No Point Treaty (Mindy Rowse, Point No Point Treaty Council, 7999 NE Salish Lane, Kingston, WA 98346).

[c]EPA, Western Washington Watershed screening data, Lunetta et al. (1997).

[d]LWD = large woody debris; TFW Reports, R. Mackintosh, North West Indian Fish Commission, 6730 Martin Way E, Olympia, WA 98516; Mindy Rowse, Point No Point Treaty Council, 7999 NE Salish Lane, Kingston, WA 98346).

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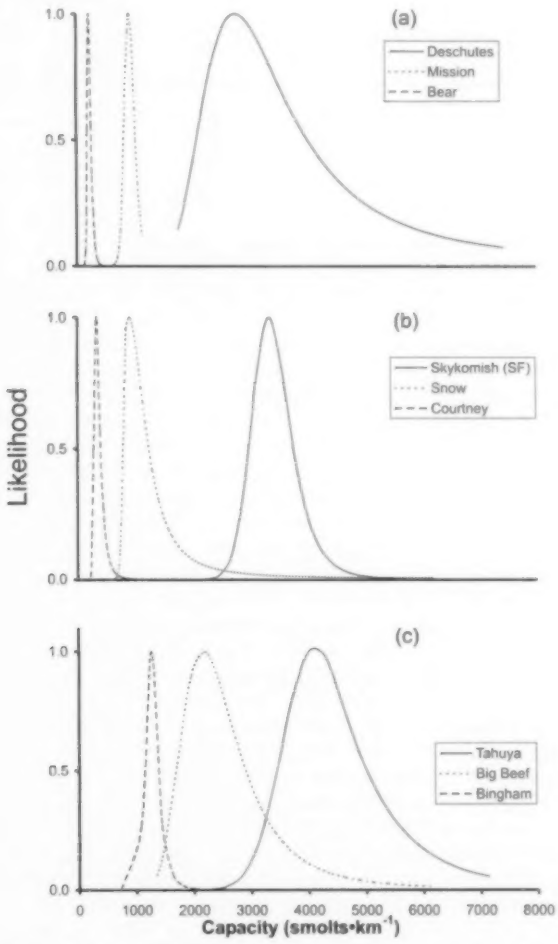
Table 4. Parameter estimates of productivity and capacity with confidence intervals (CI) using the Beverton–Holt equation.

Locations	Productivity, smolts·female^{-1} (95% CI)	Capacity, smolts·km^{-1} (95% CI)
Big Beef Creek	146 (100–600)	2156 (1340–3659)
Snow Creek	71 (52–106)	910 (739–1818)
Bingham Creek	na (na)	1236 (112–1351)
Deschutes River	51 (35–83)	2745 (1852–5926)
S.F. Skykomish River	247 (130–850)	3352 (2706–4058)
Bear Creek	na (na)	218 (165–297)
Mission Creek	na (na)	915 (766–1109)
Little Tahuya Creek	na (na)	4145 (3022–6259)
Courtney Creek	na (na)	323 (258–499)

Fig. 2. Profiles indicating the capacities (smolts·km^{-1}) of the various streams.



where S_t is the number of smolts counted in year t, E_{t-2} is the escapement of female spawners in year $t–2$, p is the initial slope of the line or the number of smolts per female at low density, and c is the maximum number of smolts that can be produced by the stream. For streams for which counts of female spawners and subsequent smolts were available, we used the method of maximum likelihood (Hilborn and Mangel 1997) to estimate the parameters p and c.

We predicted the smolt count from the spawning numbers as a function of eq. 1 and values of p and c assuming that the observations are log-normally distributed. The log-normal assumption is usually deemed appropriate for these relationships because of the multiplicative nature of survival between egg deposition and smolt counts (Hilborn and Walters 1992). The likelihood of observing S_t smolts given the predicted value is

$$(2) \qquad L(S_t|p,c) = \frac{1}{\sqrt{2\pi\sigma^2}} \frac{1}{(S_t)} \exp\left[-\frac{(\ln(S_t) - \ln(\hat{S}_t))^2}{2\sigma^2}\right]$$

where $\hat{S}_t$ is the predicted number of smolts from eq. 1 given p, c, and E. The total likelihood is simply the product of each of these over all t where data are available.

The method of likelihood profile (Hilborn and Mangel 1997) was used to calculate confidence intervals (CI) for p and c. We could estimate both p and c for streams for which absolute spawner counts were available (five streams). For the remaining four streams with only index spawning counts, the units of p were not interpretable because the absolute number of female spawners on the system was unknown, but c could be estimated.

The relationship between stream and watershed variables and smolt abundance

We used a linear regression between smolt output and habitat variables to examine the relationship between smolt abundance and habitat characteristics:

$$(3) \qquad P_s = \alpha + \beta V_{i,s} + \varepsilon_s$$

where P_s is smolts·km^{-1} in stream s, $V_{i,s}$ is the independent stream or watershed variable (pool density, pond density, road density, etc.) in stream s, α is a constant, β is the slope parameter of the variable ($V_{i,s}$), and ε is the normal additive error.

We used the normal likelihood to find the best estimates of our parameters:

$$(4) \qquad L(P_s|\alpha,\beta) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{((P_s) - (\hat{P}_s))^2}{2\sigma^2}\right]$$

Likelihood profiles were generated on the slope parameter using eq. 4. We know that on a reach scale, the habitat variables (pool density, pond density, and large woody debris (LWD)) are positively correlated with smolt abundance, and for the pool and pond densities, we expect that the slope parameter will be significant. However, we do not know how the watershed variables or the index of land use will correlate with smolt abundance. We performed analyses with each variable independently as some of the stream habitat and watershed variables are highly correlated.

Rather than look at a traditional approach of statistical inference, i.e., significance or nonsignificance of a particular variable

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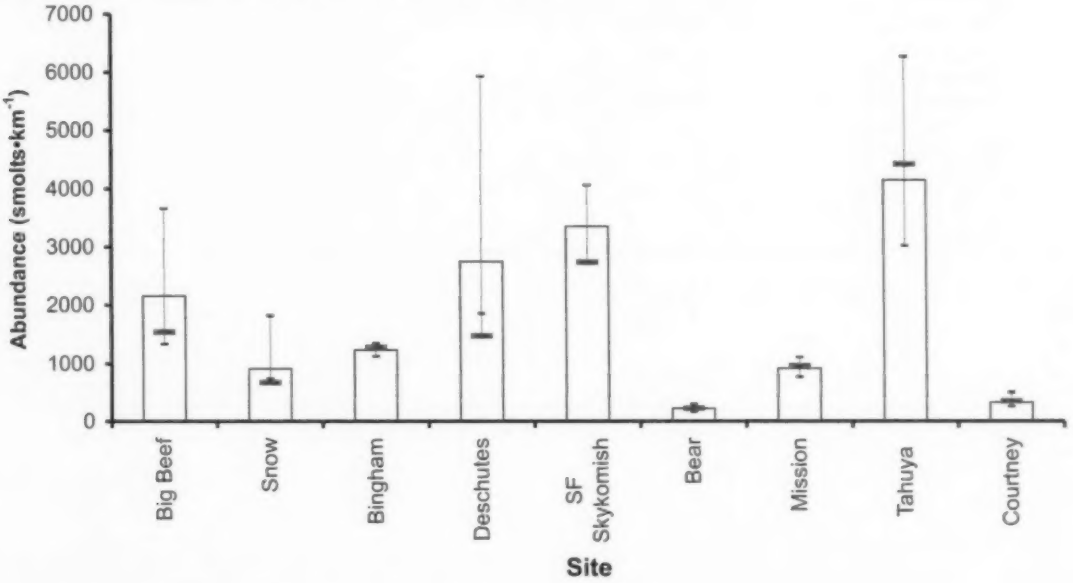
Fig. 3. Comparisons of the mean smolt abundances to the capacities for the nine streams where spawner and smolt data were available. The histogram represents the capacity, the thin line indicates the confidence bounds on the capacity estimate, and the solid bar on the line indicates the observed mean of the data for a particular stream.



(the value of the β parameter in eq. 3), we performed a likelihood profile analysis on each independent variable (Hilborn 1997).

Results

Spawner–recruit analysis results

We obtained estimates of productivity and capacity (Table 4). Productivity varied from 50 smolts per female on Deschutes River to 246 smolts per female on Skykomish River. We could not estimate the Bingham Creek productivity because of the very poor fit to the curvilinear shape of eq. 2. The likelihood profiles for the capacity parameters (Fig. 2) are rescaled with the highest likelihood of a specified capacity for that particular stream. Capacities measured as smolts·km^{-1} varied considerably and the stream with the highest smolts·km^{-1} was Little Tahuya Creek (4145 smolts·km^{-1}) in Hood Canal, and the lowest was Bear Creek (218 smolts·km^{-1}).

Ideally, p and c obtained from the spawner–recruit data could be correlated with the stream and watershed variables. However, because we had only five streams with absolute female escapement data, we instead analyzed correlations between habitat variables and the average number of smolts produced from each stream, increasing our sample size to 14 streams for some of our watershed variables. Average smolt abundance compared fairly well with the capacities obtained from our analysis (described above) (Fig. 3). In almost all cases, the observed mean of the data lies within the 95% confidence bounds of the parameter estimate (other than Deschutes River and Snow Creek).

Linear model analysis

Some of the habitat variables were highly correlated, and therefore an analysis was done with each watershed and stream habitat variable independently (Fig. 4), recognizing that the correlation between habitat variables may explain the correlation between those variables and smolt abundance. Among all variables examined, the best correlation with smolt density was obtained from pool density (r^2 = 0.85). The likelihood profile of β (Fig. 5) is explained in some meaningful modification of watershed attribute for each parameter. These figures contain far more information than either a point estimate of the slope or a traditional p value. For instance, we can observe that stream gradient, valley slope, pool and pond densities, and LWD are correlated with smolt abundance. The biological significance can be judged by examining the x-axis, in each case relating the amount of additional smolt abundance to be expected by an increase in the habitat variable. Figure 5 illustrates the uncertainty of the fit and how likely we are to see a particular effect as compared with other hypothesized effects. A standard frequentist method would provide the slope parameter and confidence bounds (this, however, gives you no information on the distribution of probability within that interval). In contrast, the likelihood profile (Fig. 5) shows us the uncertainty around the point estimate and how likely some value may be with respect to another slope value. Therefore, in the case of our analysis, other variables that may not be statistically significant, such as gradient, valley slope, LWD, and road density, still show an effect on smolt abundance (Fig. 5). These profiles illustrate the possible effects of different independent variables on our predicted variable and also illustrate the uncertainty around the best fit.

Smolt abundance declines with increasing gradient and valley slope (Fig. 4). The likelihood profiles of these variables (Fig. 5) also indicate a likely reduction in smolt abundance as higher-gradient tributaries are examined. The results suggest a 400 smolts·km^{-1} increase per 1% decrease

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Fig. 4. Best fits for the response variable (smolts·km^{-1}) with separate predictor variables: (*a*) gradient; (*b*) valley slope; (*c*) pool density; (*d*) pond density; (*e*) large woody debris (LWD) density; (*f*) drainage density; (*g*) road density; and (*h*) lake density.

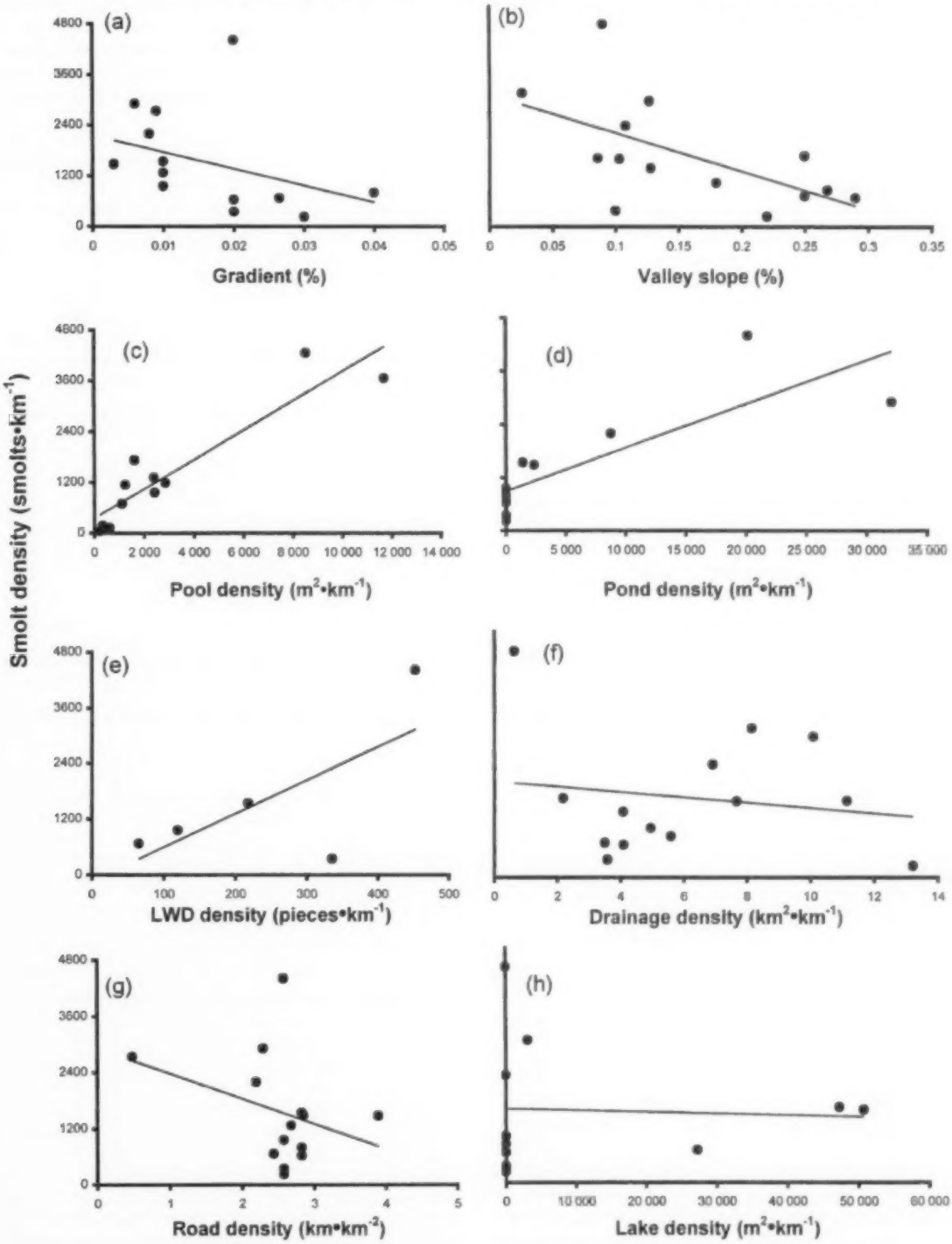

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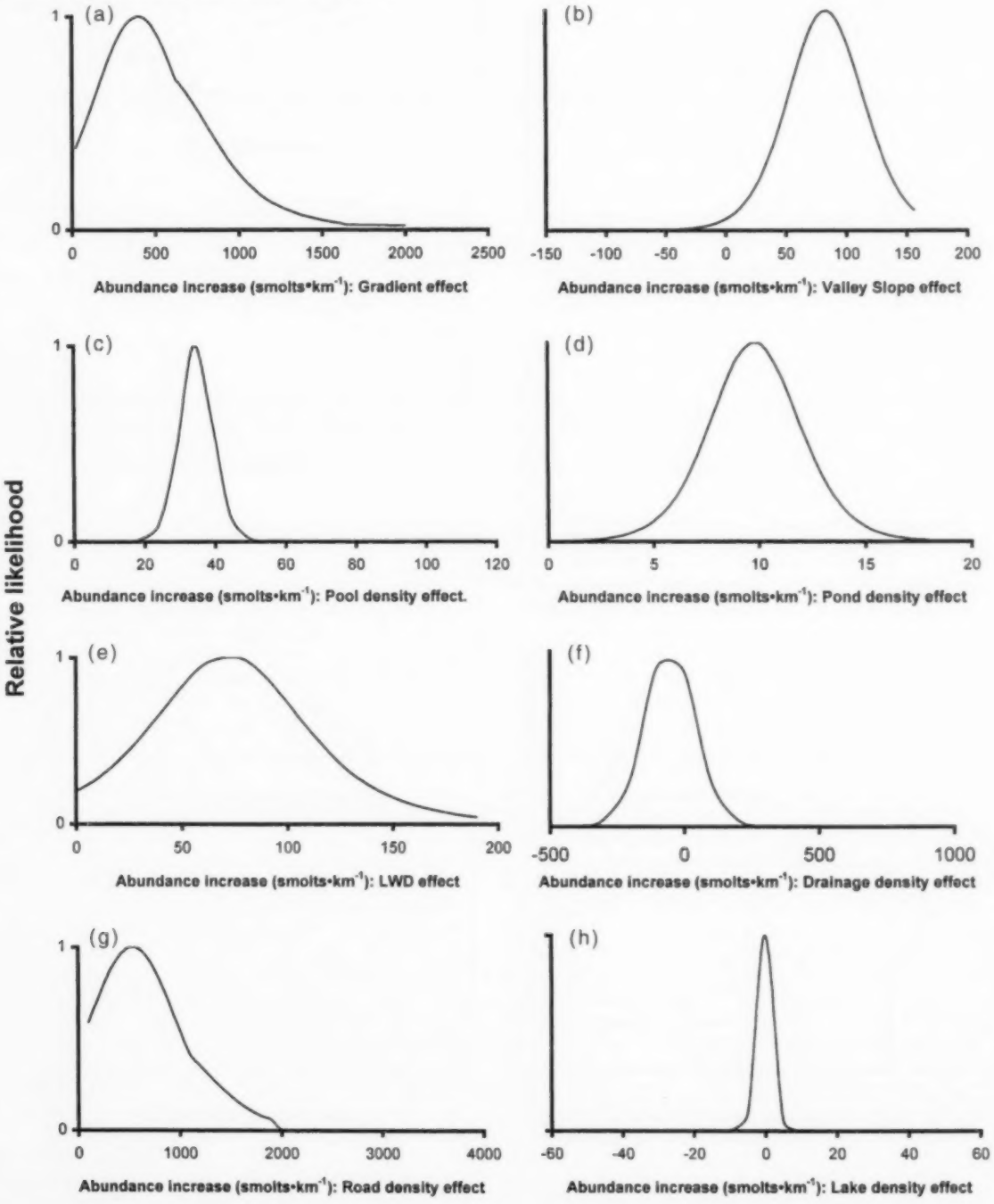
Fig. 5. Likelihood profiles of quantitative changes in smolt density as the result of increasing or decreasing some predictor variables (the *x*-axis shows the expected increase or decrease in abundance (smolts·km^{-1}) with change in the predictor variable): (*a*) gradient, the increase in abundance per percent decrease in gradient; (*b*) valley slope, the increase in abundance per percent decrease in valley slope; (*c*) pool density, the increase in abundance per increase in pool area by 100 m^2·km^{-1}; (*d*) pond density, the increase in abundance per increase in pond area by 100 m^2·km^{-1}; (*e*) large woody debris (LWD) density, the increase in abundance per 10 additional pieces of LWD·km^{-1} of stream; (*f*) drainage density, the increase in abundance per increase in drainage area by 1 km^2·km^{-1} of stream length; (*g*) road density, increase in abundance per decrease in road density by 1 km·km^{-2} in the watershed; and (*h*) lake density, the increase in abundance per increase in lake area by 100 m^2·km^{-1}.



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in gradient and an 84 smolts·km^{-1} increase per 1% decrease in valley slope. This result is not surprising as coho salmon tend to spawn and rear in lower-gradient tributaries (Bisson et al. 1988).

Although there were very few streams with LWD data, the results were interesting and suggested an additional 7 smolts·km^{-1} (Fig. 5) for every additional LWD·km^{-1}. We can observe that the profile for LWD is the flattest, thus illustrating the uncertainty surrounding additional pieces of LWD and the hypothesized effect that one would expect to observe on streams with higher LWD concentration. Road density had a negative correlation with smolt abundance, but this was largely due to the outlying points in the data set. The results suggest a decrease of 500 smolts·km^{-1} for each 1 km·km^{-2} increase in road density. However, no effect is about half as likely as observing the above-stated effect. These profiles illustrate the uncertainty in the estimate of β and the possible distribution of effects likely to be observed on streams in this particular watershed.

The watershed variable drainage density and the stream-habitat variable lake density show no correlation with smolt abundance, whereas road density is negatively correlated with smolt abundance. Drainage density and lake density slopes are centered on zero (Fig. 5). This suggests that perhaps these variables are not really important for coho juvenile survival. Even though some juvenile coho use lakes to rear, it appears that these variables in the systems studied did not show any significant relationships.

Discussion

Although low adult spawner abundance in river systems in Puget Sound is being blamed for the lower cohort abundance in corresponding years (time series observed in the 1980s and early 1990s), the data suggest otherwise. It has been shown that the average smolt abundance on most of these streams lies within the confidence bounds (95% CI) for the capacity of smolt abundance estimated in these streams through standard likelihood estimation techniques. Hence, the streams appear not to be spawner limited (other than Deschutes River and Snow Creek) but may instead be limited by some other factor.

Nickelson et al. (1992*a*) emphasized that pool and pond areas were the limiting factors to smolt abundance in seeded streams in Oregon. In addition, he computed the capacity of fry in different types of pool habitat (Nickelson et al. 1992*b*). However, we did not have the pool habitat broken down further into Nickelson's subcategories by season. Nickelson's results show that on average the number of smolts is about 0.4 smolts·m^{-2} of pool area over the year and 1.8 smolts·m^{-2} of pond area over the year. Our results from a multiple regression analysis using pool and pond densities, which explained 92% of the residual error, were 0.4 smolts·m^{-2} of pool area and 0.07 smolts·m^{-2} of pond area (correlation between pool and pond densities was high, however, with $r = 0.47$) in summer. Unfortunately, we did not have stream data that would compare with Nickelson's results for the entire year as done in Oregon, and therefore, the ponds' true effect might be underestimated. Both studies, however, obtain very similar values for the effect of pool areas on smolt abundance. A possible reason for this difference in pond effects may be due to the fact that Nickelson's studies were conducted on Oregon coastal streams with a steeper gradient. These streams are extremely vulnerable to high flow events in winter, and side-channel habitat (side-channel ponds) is extremely important in these coastal streams. This may not be the case for Puget Sound streams, which are somewhat protected from extremely high flow events by the Olympic mountains located to the west of Puget Sound.

The streams in Washington do not appear to be spawning limited as the average smolt abundance on these streams lies within the 95% CI of the capacity. However, the capacity does vary and a clear correlation between average smolt abundance and summer pool density has been established. For most of the summer stream and watershed variables analyzed, the summer pool areas had the strongest correlation with the smolt abundance. This implies that summer pool area is one of the limiting factors of smolt abundance on western Washington streams. Ponds typically provide refuge during high winter flows, and the low value of smolts produced per pond area in our analysis suggests that these habitats are less important than summer pools for the watersheds studied. However, because we did not have stream data for the entire year, this effect may be underestimated. Both pools and ponds are, however, complexly intertwined as side channel ponds are extremely important for overwintering (Nickelson et al. 1992*a*).

The major weakness of our study is the correlation between habitat factors. Pool density, pond density, and LWD·km^{-1} are all highly correlated, and one cannot simply say that increasing any one of these would increase smolt production by itself. Despite this autocorrelation, it is known that pools by themselves are just one part of the overall determinant of coho abundance. Pools with habitat structure in the form of LWD generally contain far more coho than pools without this form of cover and shelter. LWD appearing elsewhere in the channel, i.e., nonstructural LWD not in association with pools, may have little or no role in influencing fish numbers. This study was not conducted at the scale of resolution to separate out the contribution of LWD; however, the point that pool habitat is the prime and proximal determinant of juvenile coho salmon abundance can still be made. Studies such as that of Bisson et al. (1988) show similar findings.

In addition, low gradient areas tend to have more coho juveniles present because they have more pools than steeper cascades and low valley slope normally provides abundant side-channel rearing areas such as ponds. Nickelson et al. (1992*a*, 1992*b*) and Beechie and Sibley (1997) have shown similar results on a stream-specific basis.

This analysis allows us to calculate the possible increase in smolt production resulting from different forms of habitat modification. However, this is subject to the limitation that we assume the streams are not spawning-stock limited, and all other factors are comparable with those of the streams in the data sets used.

This method could provide valuable insight into which areas to target for habitat restoration by showing us where habitat restoration activities are likely to have the greatest effect on smolt abundance at the watershed level. We can observe that where pool areas can be increased substantially, coho salmon smolt abundance is likely to increase. This activity is most feasible on lower-gradient and valley slope

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systems. Thus, effects of in-stream habitat modification on smolt abundance could be hypothesized and, after post-treatment experiments, evaluated with this benchmark.

A complete computational framework for evaluating the benefits of habitat improvement will need to include spawning stock availability and factors beyond habitat limitation on rearing capacity (e.g., Beechie et al. (1994) and Reeves et al. (1989)). Nickelson and Lawson (1998) also take this approach a step further by looking at population viability. However, the simpler approach shown here could serve as a tool for formulating pretreatment hypotheses on watersheds where such data are not available. In addition, data such as pool and pond densities could be collected fairly easily on a watershed level and, using this simple regression model, could help in understanding the limiting factors of freshwater rearing. We could also use this simplified approach to estimate juvenile abundance in the particular streams of a region. In today's realm of endangered species, this is a useful tool in understanding the limitations of habitat and how it might relate to juvenile abundance of salmon.

Bradford et al. (1997) found that smolt abundance was best explained by stream length and latitude. We have moved beyond Bradford's analysis by looking at smolt abundance per kilometre of stream and found that a number of habitat factors are related to smolt abundance. By looking only within Puget Sound, we may have eliminated some of the variability that Bradford found in his geographically broader analysis. Although there should be little surprise that the habitat factors such as pool and pond area are related to smolt abundance, this study is the first to relate downstream smolt counts to watershed and stream attributes averaged across small watersheds.

In conclusion, this approach could be a valuable tool for habitat restoration planning as well as for estimating likely increases in juvenile salmon abundance (for this case, in western Washington and Hood Canal streams). This technique could provide insight into the likely effects that various habitat-enhancement measures may have on the particular stream in that watershed or basin.

Acknowledgments

We wish to thank Tim Beechie, Peter Tchaplinski, and the reviewers for their valuable insight on habitat issues relevant to the paper. Dr. Tom Quinn and Dr. Dan Huppert are also acknowledged for their valuable input in development of this analysis, as well as the Washington Sea Grant Program for funding this project.

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What is the carrying capacity for fish in the ocean? A meta-analysis of population dynamics of North Atlantic cod

Ransom A. Myers, Brian R. MacKenzie, Keith G. Bowen, and Nicholas J. Barrowman

Abstract: Population and community data in one study are usually analyzed in isolation from other data. Here, we introduce statistical methods that allow many data sets to be analyzed simultaneously such that different studies may "borrow strength" from each other. In the simplest case, we simultaneously model 21 Atlanic cod (*Gadus morhua*) stocks in the North Atlantic assuming that the maximum reproductive rate and the carrying capacity per unit area are random variables. This method uses a nonlinear mixed model and is a natural approach to investigate how carrying capacity varies among populations. We used empirical Bayes techniques to estimate the maximum reproductive rate and carrying capacity of each stock. In all cases, the empirical Bayes estimates were biologically reasonable, whereas a stock by stock analysis occasionally yielded nonsensical parameter estimates (e.g., infinite values). Our analysis showed that the carrying capacity per unit area varied by more than 20-fold among populations and that much of this variation was related to temperature. That is, the carrying capacity per square kilometre declines as temperature increases.

Résumé : Les données provenant d'études démographiques ou biocénotiques sont habituellement analysées séparément les unes des autres. On trouvera ici des méthodes statistiques qui permettent l'analyse simultanée de plusieurs séries de données de façon à ce que les différentes études se renforcent mutuellement. Le cas le plus simple consiste en une modélisation simultanée de 21 stocks de morues franches (*Gadus morhua*) de l'Atlantique nord qui présume que le taux maximal de reproduction et la capacité limite par unité de surface sont des variables aléatoires. La méthode utilise un modèle mixte non-linéaire et elle se révèle être une stratégie naturelle pour l'étude de la variation de la capacité limite chez les populations. Des techniques empiriques bayésiennes ont servi à estimer le taux maximal de reproduction et la capacité limite de chaque stock. Dans tous les cas, les estimés obtenus sont biologiquement vraisemblables; en revanche, des analyses faites stock par stock génèrent à l'occasion des estimations absurdes (e.g., des valeurs infinies). Nos analyses montrent que la capacité limite par unité de surface varie d'un facteur de plus de 20 d'une population à une autre et qu'une partie importante de cette variation est reliée à la température. En effet, la capacité limite par kilomètre carré décline à mesure que la température augmente.

[Traduit par la Rédaction]

Introduction

Understanding the relationship between the abundance of mature fish (spawners) and the production of new replacement fish (recruitment) is essential for management decisions such as determining catch quotas, making prognoses of how the stock will react to different fishing levels or closures, setting biological reference points such as critical stock levels below which fishing should be banned, and estimating stock extinction probabilities.

One of the most common ways to investigate spawner–recruitment relationships is to fit a spawner–recruitment model, e.g., a Ricker or a Beverton–Holt model (more generally known as a Michaelis–Menten model), for a single stock. Unfortunately, this approach has some serious limitations. First, relationships between spawner abundance and recruitment for single stocks are usually poorly defined and characterized by high uncertainty (Myers et al. 1994). Because these statistical relationships are uncertain, derived biological reference points are also uncertain and it can be difficult to forecast the consequences of reduced stock size.

Second, considering stock dynamics on an individual-stock basis does not allow for the possibility that including information from other stocks might yield superior parameter estimates of spawner–recruitment relationships in local areas. Alternative statistical methods, including meta-analysis and Bayesian approaches, that "borrow strength" from other populations or stocks can be used to improve parameter esti-

Received August 22, 2000. Accepted April 11, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 21, 2001.
J15937

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 DOI: 10.1139/cjfas-58-7-1464 © 2001 NRC Canada

mates for a given stock (Hilborn and Liermann 1998; Myers and Mertz 1998*b*; Dorn 2001).

Third, considering only one stock at a time and in units that are not standardized among stocks makes it impossible to compare productivities, carrying capacities, and other biological factors among stocks and ecosystems. If the spawner–recruitment data are standardized in such a way that the indices of carrying capacity, e.g., the asymptotic recruitment in the Beverton–Holt model, can be considered to be on the same scale, then it may be possible to "borrow strength" to improve estimates. Methods to improve estimates of carrying capacity may help to resolve some long-standing problems in marine ecology. Standardizing units among stocks can also be used to produce inputs for ecosystem models, such as ECOPATH, that use production per unit area (Walters et al. 1997; Christensen and Pauly 1998).

In this article, we consider the spawner–recruitment problem from a meta-analytical and comparative perspective. Our objectives are to (*i*) introduce alternative statistical methods to improve spawner–recruitment parameter estimates for individual stocks and (*ii*) use these methods to begin comparing carrying capacities in different ecosystems.

Materials and methods

Data

Spawner abundance, recruitment, and biological data were obtained from the compilation in Myers et al. (1995) and Myers et al. (1999) (Table 1). The recruitment and spawner data were standardized to common units in the following two ways.

We standardized the recruit data by multiplying the recruit numbers-at-age by an estimate of the numbers of spawners produced per recruit when fishing mortality is 0, $SPR_F = 0$ (Mace 1994; Myers and Mertz 1998*a*). The product of recruitment and $SPR_F = 0$ expresses the lifetime recruitment or the biomass of spawners that a single recruit can produce during its lifetime in the absence of fishing. At equilibrium, this quantity can also be interpreted as the annual mean spawning biomass present in the unfished population. The standardization only transforms the units of the data and does not alter the relative rankings of the recruitment data.

We have not included recent data from Atlantic cod (*Gadus morhua*) stocks in Canada because of the difficulty of assessing these stocks with no catch-at-age data. Furthermore, the survey methods for most of the Canadian stocks changed drastically after the 1995 moratorium on cod fishing, which makes the data even more difficult to assess.

We also standardized the data for differences in area of juvenile habitat among the different geographic regions. This standardization was done to remove the influence of differences in size of the region occupied by the different stocks, since larger areas could potentially support larger populations. We standardized by dividing the recruits and spawners by the area. Juvenile habitat size is not as well described for cod as it is for other species such as European plaice and sole (Rijnsdorp et al. 1992). For our purposes, we initially assume that juvenile cod habitat area was all ocean bottom between the 0 and 300 m depth. This is an oversimplification but probably is correlated with the true habitat available in the different regions. This is viewed as a first step in a more complex analysis.

In general, we used the area of the sea bottom between 0 and 300 m in the North Atlantic Fisheries Organization/International Council for the Exploration of the Sea (NAFO/ICES) management unit as our definition of habitat. However, habitat for three stocks did not fit this definition. Icelandic cod juveniles often use the coast of Greenland during the first few years of their life (Hovgard and Buch 1992). We thus used the area around Iceland (ICES Va) and southern Greenland (ICES XIVb) as juvenile habitat for this stock. For Barents sea cod, the area of habitat appears to be limited by cold temperatures (Ottersen et al. 1994). Therefore, we only considered parts of ICES I that were below 78°N (Ottersen et al. 1998) and all of ICES IIa as potential habitat. Similarly, for central Baltic cod, ICES areas 30–32 are rarely used by cod because salinities are too low for successful reproduction (Nissling and Westin 1991). Habitat area for this stock was instead confined to ICES Subdivisions 25–29.

Mean annual shelf bottom temperature was estimated by Brander (1994) for all of the populations except in the Baltic. We used data in Dickson et al. (1992) to estimate bottom temperatures for the Baltic populations. We estimated independent temperatures for the Northwest Atlantic from deYoung et al. (1994). Differences in temperature between these two sources were small (less than 2°C) and did not have an important effect on our findings. Our analyses thus describe and quantify spawner–recruit parameters on a per area basis.

Models

For the cod populations, we consider Beverton–Holt models. The approach that we use can easily be applied to alternative models, including those with more parameters. Suppose we have M stocks and suppose that for stock i, we have n_i observations for $i = 1,..., M$. The n_i observations for stock i are of the form (S_{ij}, R_{ij}), $j = 1,..., n_i$, modeled as

$$(1) \qquad R_{ij} = \frac{\alpha_i S_{ij}}{1 + S_{ij}/K_i} e^{\varepsilon_{ij}}$$

where $\alpha_i > 0$ and $K_i > 0$, and $\varepsilon_{11}, ..., \varepsilon_{Mn_M} \overset{iid}{\sim} N(0, \sigma^2)$. The simplest biological interpretation of the slope at the origin, α_i, is that it is the average rate at which replacement spawners are produced per spawner over the spawner's lifetime at low abundance in the absence of anthropogenic mortality (after a time delay for the age at maturity) (Myers et al. 1999). Ecologists term this the maximum reproductive rate. The K_i is the spawner biomass that results in an average recruitment of half the average asymptotic recruitment, which is given by $\alpha_i K_i$. In this model, the carrying capacity is the equilibrium spawner abundance if no fishing occurs, i.e., at the intersection of the above equation with the replacement line (which is the 1:1 line here because we have standardized recruitment). In the Discussion, we will approximate this as the asymptotic recruitment, $\alpha_i K_i$, in our transformed units of spawning biomass.

Note that we have initially assumed that the error variance (σ^2) is constant across stocks. This is the simplest possible assumption about the residuals, which are due to environmental effects and observational errors (Table 2); more complicated models are considered below. Taking logarithms gives

$$\log R_{ij} = \log \alpha_i + \log S_{ij} - \log(1 + S_{ij}/K_i) + \varepsilon_{ij}.$$

Define $y_{ij} = \log(R_{ij}/S_{ij})$, $\log \alpha_i = a + b_i$, and $\log K_i = c + d_i$, giving

$$y_{ij} = a + b_i - \log(1 + S_{ij}/\exp(c + d_i)) + \varepsilon_{ij}.$$

Note that modeling the logarithms of α_i and K_i constrains α_i and K_i to be positive.

Model 0 (individual data sets model)

Treat $a, b_1,...,b_M, c, d_1,...,d_M$ as fixed. This is the standard model used in population ecology. It is based on the unrealistic assumption that there is no relationship among populations of a taxonomic group.

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Table 1. Cod populations used in the analysis identified by geographical area and NAFO/ICES management units and the area of shelf between 0 and 300 m depth, mean annual shelf bottom temperature, and number of pairs of spawner–recruit observations used in the analysis (n).

Stock	NAFO/ICES	Area (km^2)	Temperature (°C)	n
Labrador and Northeast Newfoundland	2J3KL	253 492	0	28
Southern Grand Banks	3NO	121 246	1.75	31
Northern Gulf of St. Lawrence	3Pn4RS	89 041	1	17
St. Pierre Bank	3Ps	70 510	2.5	31
Southern Gulf of St. Lawrence	4TVn	118 343	1.75	41
Eastern Scotian Shelf	4VsW	102 428	3.75	33
Southwest Scotian Shelf	4X	77 634	6.75	45
Gulf of Maine	5Y	95 582	8	7
Georges Bank	5Z	102 596	8	18
Westrn Baltic	BA2224	43 913	7	22
Central Baltic	BA2529	216 833	5	24
Celtic Sea	VIIe-f	155 358	11	22
Faroe Plateau	Vb1–2	36 236	7.4	33
Iceland	Va/XIVb	237 031	5.8	68
Irish Sea	VIIa	48 263	10	27
Kattegat	IIIa (south)	17 362	6.5	21
Northeast Arctic	I,II	592 610	4	43
North Sea	IVa-c	539 823	8.6	30
Skagerrak	IIIa (north)	11 345	6.5	13
Eastern English Channel	VIId	32 067	9.6	18
West of Scotland	VIa	105 666	10	27

Table 2. Results for four REML estimates using Model III for all cod stocks simultaneously.

Model	Error variance	Random effects correlation	Estimates		Standard error		Random effects variance		Parameters estimated	log likelihood
			log α	log αK	log α	log αK	log α	log αK		
a	Single	Yes	3.52	2.53	0.24	0.25	0.76	0.99	6	–584.47
b	Multiple	Yes	3.57	2.52	0.22	0.24	0.66	0.96	26	–535.84
c	Single	No	3.52	2.53	0.24	0.25	0.76	0.98	5	–584.48
d	Multiple	No	3.56	2.52	0.22	0.24	0.67	0.96	25	–535.82

Note: Alternative assumptions are made for the error variance, i.e., that it was the same for all stocks or was estimated separately for each stock, and for the correlation between the random effects, i.e., no correlation or a correlation that is estimated from the data.

Model I (random α's, fixed K's model)

Treat a, c, d_1,..., d_M as fixed; assume b_1,..., $b_M \overset{\text{iid}}{\sim} N(0, \sigma_b^2)$. This model produces good results (i.e., biologically and statistically meaningful estimates) for linear (i.e., Ricker) spawner–recruitment functions (Myers et al. 1999), but often not in the nonlinear case unless sufficient data exist at all levels of spawner abundance. Model I may also lead to estimation difficulties because of the large number of fixed effects. Furthermore, because each additional stock introduces an additional nuisance parameter, the asymptotic properties of estimators for such models are nonstandard. Jiang (1996) has studied the asymptotic properties of estimators for linear models of this type; however, results have not been obtained in the nonlinear case.

Model II (random α's and K's model)

Treat a and c as fixed and assume

$$\begin{pmatrix} b_i \\ d_i \end{pmatrix} \overset{\text{iid}}{\sim} N\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_b^2 & \sigma_{bd} \\ \sigma_{bd} & \sigma_d^2 \end{pmatrix}\right], \quad i = 1, \ldots, M.$$

It is important to recognize that Model II requires not only a standardization of recruits (so that the α's are in the same units for each stock) but also a standardization of spawner abundance (so that the K's are in the same units for each stock.) These standardizations were described in the previous section.

Model III (random α's and αK's model)

We can rewrite eq. 1 as

$$(2) \qquad R_{ij} = \frac{S_{ij}}{1/\alpha_i + S_{ij}/(\alpha_i K_i)} e^{\varepsilon_{ij}}$$

which leads to

$$y_{ij} = -\log(1/(a + b_i) + S_{ij}/\exp(e + f_i)) + \varepsilon_{ij}$$

where $e = a + c$ and $f_i = b_i + d_i$, so that $e + f_i = \log(\alpha_i K_i)$. Treat a and e as fixed and assume

$$\begin{pmatrix} b_i \\ f_i \end{pmatrix} \overset{\text{iid}}{\sim} N\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_b^2 & \sigma_{bf} \\ \sigma_{bf} & \sigma_f^2 \end{pmatrix}\right], \quad i = 1, \ldots, M.$$

Model IV (random α's and αK's with an additional systematic component)

The maximum reproductive rate, α, or the asymptotic recruitment, αK, may have a systematic as well as a random component.

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For example, the maximum reproductive rate of sockeye salmon (*Oncorhynchus nerka*) appears to be lower at the northern part of its range (Myers et al. 1999). In such cases, we can still consider α's and αK's as random variables but allow for a systematic component as well. We will illustrate each of the above five models with an example in a subsequent section.

We consider Models II, III, and IV here because comparative and simulation analysis suggests that they perform much better than Models 0 and I (Barrowman 2000). Another model is to use an inverse transformation and gamma errors; we will return to this in the section on alternative formulations.

For each of the models above (II, III, and IV), we consider two alternative assumptions: (*i*) the error variance differs among stocks and (*ii*) the random variables are correlated.

Approaches to inference

Nonlinear mixed effects models belong to the general class of hierarchical models. Recently, the hierarchical Bayes approach has enjoyed considerable popularity because it permits estimation of a very broad class of models and may produce more realistic assessments of the uncertainty of parameter estimates. However, this approach requires specification of a joint prior distribution for the fixed effects and variance components. Even if the joint prior is assumed to decompose into a product of marginal priors, the task may be challenging. Furthermore, estimation, typically done using Markov Chain Monte-Carlo (MCMC) methods, can be time consuming and determination of convergence may be difficult.

A traditional mixed effects model approach is an alternative, and software currently exists for both linear and nonlinear models of this type if Gaussian errors and random variables are assumed. Here, we concentrate on this approach because of its relative simplicity and reliability. We obtain estimates for our models using the approximate maximum likelihood algorithm of Lindstrom and Bates (1990). The output from our analyses could serve as starting values and checks in a hierarchical Bayes approach.

In many cases, the focus of inference is not limited to the fixed effects and variance components; estimates of realized values, say for an individual stock, of the random effects (traditionally, although misleadingly, called "predictions") are also of interest. Commonly, empirical Bayes estimates are used for this purpose. The reason for this terminology comes from considering the distributions of the random variables as prior distributions. If the parameters of the prior distributions (i.e., the variances and covariances) were known, then standard Bayesian calculations would give posterior distributions for the random variables, and point estimates could be obtained using, for example, posterior means. The best linear unbiased predictor (BLUP) in a linear mixed model may be derived in this way (Dempfle 1977). Since the parameters of the priors are unknown, the empirical Bayes approach is to substitute estimates of the parameters of the prior distributions and then proceed as if using true prior distributions. The empirical BLUP (used, for example, by Myers et al. (1999)) is an example of this. In the present work, the empirical Bayes estimates are the estimated posterior modes for the random variables provided by the Lindstrom and Bates (1990) algorithm.

The nonlinear mixed effects model is used to estimate the parameters of the random effects for the population of 21 stocks. Estimates of realized values of the random effects for individual stocks are obtained by combining the information from the population of stocks with the point estimate for that stock. The resultant estimate is "shrunk" towards the population mean. For linear mixed models, this is analogous to a weighted average, with weights inversely proportional to the variance.

The hierarchical Bayes approach instead puts prior distributions on the parameters of the random variables distributions (the so-called hyperparameters), which are often called hyperpriors. We sometimes refer to the hierarchical Bayes approach as "fully Bayes" to distinguish it from the empirical Bayes approach and hybrid approaches involving specification of prior distributions for some but not all parameters (e.g., Liermann and Hilborn 1997). Hierarchical Bayes approaches are commonly implemented today using MCMC algorithms. If the hyperpriors are uninformative and the marginal likelihood of the hyperparameters is relatively peaked, the empirical Bayes and fully Bayes approaches should give similar results (Smith 1983).

In the complex problems that we are dealing with, there are potential technical difficulties with all approaches. For example, in the fully Bayes approach, it is often difficult to (*i*) determine if an MCMC algorithm has converged, (*ii*) choose truly uninformative proper hyperpriors (improper priors (or hyperpriors) may result in unreliable inference (Hobert and Casella 1996)), and (*iii*) compare the relative fit of different models. The empirical Bayes approach that we use here also has potential difficulties. For example, approximations to integrals that are often used may not be adequate and the variances of the estimates will be underestimated (Efron 1996). For these reasons, we believe that a comprehensive analysis will make use of both approaches.

Results

Mixed effects model

We begin by examining different model formulations to determine which model specification to use in the subsequent empirical Bayes analyses. Specifically, we examined (*i*) Model II versus Model III, (*ii*) assumptions about the correlations between the random variables, i.e., $\log K$ and $\log \alpha$, and (*iii*) the variance in error (which is either the same for all populations or different for each).

First, we compare Models II and III. When we allow the random effects in these models to be estimated from the data, the two models give very similar results and goodness of fit estimates, regardless of whether the random variables are correlated or not. However, if we fix the correlation between the random variables to be zero, Model III always gives superior fits compared with Model II, i.e., the maximized likelihood was always greater. Thus, we will restrict our attention to Model III.

We used restricted maximum likelihood (REML) to fit Model III (Table 2). REML can be thought of as an adjustment to the degrees of freedom accounting for the fixed effects, which helps to give less biased variance estimates (Searle et al. 1992). The likelihood ratio test (lrt) was used to compare the fit of different models.

We must choose between the assumption that the correlations between the random variables, i.e., $\log \alpha K$ and $\log \alpha$, are zero or not. To do so, we compare the maximum likelihood fit with and without the assumption of the correlation constrained to be zero. In no case was the improvement in fit close to being statistically significant (Model a versus Model c: lrt = 0.02, $p = 0.89$; Model b versus Model d: lrt = 0.04, $p = 0.84$). The estimated correlations between the random variables obtained from Models a and b are very low ($p < 0.02$), which explains the similar results for both assumptions.

Selecting the best model is not based solely on simple measures of goodness of fit but should be constrained by biological information. We prefer the model estimates in which the random variables are uncorrelated because there is no reason to believe that the maximum reproductive rate, α, should be correlated with αK, which quantifies carrying ca-

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Table 3. Results for standard single-species maximum likelihood estimates (individual) and empirical Bayes (EB) REML estimates using Model IIId.

	log α		log αK		
Stock	Individual	EB	Individual	EB	log K, EB
Labrador and Northeast Newfoundland	2.26	2.94	4.27	3.18	0.24
Southern Grand Banks	2.65	3.24	2.94	2.44	–0.8
Northern Gulf of St. Lawrence	2.41	3.22	2.75	2.27	–0.95
St. Pierre Bank	3.46	3.53	2.87	2.84	–0.69
Southern Gulf of St. Lawrence	26.98	3.79	1.65	1.74	–2.05
Eastern Scotian Shelf	26.9	4.1	1.98	2.21	–1.89
Southwest Scotian Shelf	27.43	3.65	1.08	1.19	–2.46
Gulf of Maine	30.32	3.46	0.84	1.51	–1.95
Georges Bank	1.85	2.5	27.12	2.23	–0.27
Western Baltic	3.51	4	6.48	3.95	–0.05
Central Baltic	3.1	3.37	3.5	3.31	–0.06
Celtic Sea	2.76	2.67	1.14	2.34	–0.33
Faroe Plateau	5.56	3.82	2.24	2.38	–1.44
Iceland	4.04	3.89	3.09	3.11	–0.78
Irish Sea	4.67	3.94	1.39	1.74	–2.2
Kattegat	3.02	3.17	3.54	3.35	0.18
Northeast Arctic	3.91	3.93	3.6	3.52	–0.41
North Sea	3.64	3.63	2.54	2.56	–1.07
Skagerrak	6.08	4.12	3.78	4.11	–0.01
Eastern English Channel	5.44	4.04	1.06	2.13	–1.91
West of Scotland	29.42	3.87	0.66	0.83	–3.04
EB mean	—	3.56	—	2.52	–1.04

Note: log K is obtained by subtraction from log α and log αK. The estimates of αK and K are given on a tonnes per square kilometre basis.

pacity among stocks. This formulation also allows for simple interpretation of the parameters. The log asymptotic recruitment appears to be less variable than the log maximum reproductive rate for all versions of Model III.

If we constrain the error variances to be the same for all stocks, then the goodness of fit, as judged by the maximized log likelihood, declines greatly (Model a versus Model b: lrt = 97.26, $p < 0.00001$; Model c versus Model d: lrt = 97.32, $p < 0.00001$). Thus, the model with multiple estimation error variances and no correlations between random variables appears to be most satisfactory (Model d in Table 2).

We display the results for a subset of stocks graphically in terms of three curves: (*i*) Model 0: the usual maximum likelihood fit to individual stocks, (*ii*) the empirical Bayes curve for each stock under mixed effects Model IIId, i.e., the curve determined by the estimates of fixed effects a and e and the estimates of the realized random effects b_i and f_i (Table 3), and (*iii*) average value for all stocks from the mixed effects Model IIId, i.e., the curve determined by taking $b_i = f_i = 0$ (Figs. 1–3). The empirical Bayes estimates for a given stock is the "optimal" estimate if all of the data are combined under the assumptions described above. The model results and data are all compared on a per kilometre basis, i.e., the differences due to variations in habitat size have been estimated.

The empirical Bayes estimates yield results that are in all cases reasonable, i.e., no effectively infinite α's or K's, as seen in some of the single stock estimates, e.g., Georges Bank and the Southwest Scotian Shelf (Fig. 2). In one case, the empirical Bayes estimate of carrying capacity was quite different from the individually fit spawner–recruitment model, i.e., for the Labrador and Northeast Newfoundland cod stock (sometimes called Northern cod or NAFO Div. 2J3KL cod) (Fig. 1). This may be an important result, as it suggests that either the stock is very unusual or the environmental conditions during the period of high recruitment (from 1959 to 1966) were unusual. We return to this point in the Discussion.

The results suggest that some stocks have higher carrying capacity per unit area (αK) than others. Another way to express the differences in stock productivity and ecosystem carrying capacity is to plot the data on common scales (Fig. 3). When plotted in this way, it is quite clear that the carrying capacity and the range of observed spawner abundances vary widely among different stocks. The variability among stocks in the slope at the origin, i.e., the maximum reproductive rate, is much less, which is consistent with the previous results of Myers et al. (1997).

For stocks where the individual ordinary least-squares fit of the Beverton–Holt models gives unreliable estimates, the empirical Bayes estimates would appear to provide satisfactory alternatives (Fig. 4).

If the individual-population estimates for α and αK are compared with empirical Bayes estimates from the mixed effects model analysis, one sees that the range of the mixed model estimates is much less than that for the single-stock estimates (Fig. 5). In particular, there is a large qualitative improvement in the fitted parameter estimates for several stocks which gave meaningless results when fitted on a single-stock basis.

In the individual-population estimates, there was one esti-

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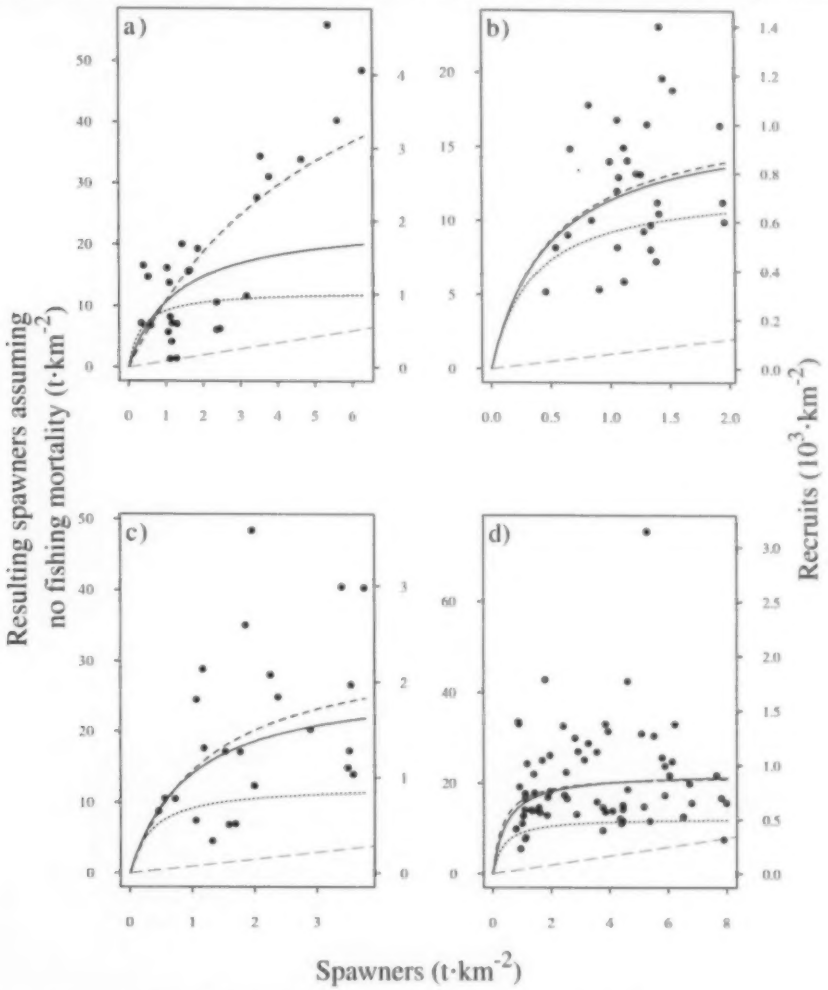
Fig. 1. Spawner–recruit relationships for cod stocks with above-average carrying capacity. (*a*) Labrador and Northeast Newfoundland; (*b*) St. Pierre Bank; (*c*) Central Baltic; (*d*) Iceland. The relationship between recruits per square kilometre and spawning stock biomass per square kilometre for two cod stocks in the Northwest and two cod stocks in the Northeast Atlantic having above-average carrying capacity (empirical Bayes estimated K values from the Beverton–Holt model). Note that axis scaling differs among stocks. Solid line: empirical Bayes estimate for the individual stock; curvilinear dashed line: single-stock maximum likelihood fit; dotted line: average estimate for all stocks from the mixed effects model (hence identical in all plots); straight dashed line: 1:1 replacement line.



mate of asymptotic recruitment αK and five estimates of α that are effectively infinite, i.e., the minimization algorithm failed to find an estimate in a feasible parameter range. In a previous study, Barrowman and Myers (2000) found similar proportions of nonfeasible estimates of these parameters in a large collection of spawner–recruit data sets.

The empirical Bayes estimates of each stock's αK value appear to vary independently of the same stock's α (Fig. 6); hence, our assumption about no correlation between random variables appears to be justified. There is also more variation in K than in α, as seen in Table 2.

In the course of the analysis detailed above, an interesting, and unsuspected, relationship became apparent. An initial data exploration indicated that there might be a relationship between asymptotic recruitment and bottom temperature that warranted further investigation. We thus use Model IV to explore this relationship. Cod stocks are split into two groups (Northwest and Northeast Atlantic) in the analysis because of the different fish communities on each side of the Atlantic. There is a strong relationship between temperature and asymptotic recruitment within each group (Fig. 7).

To obtain Model IV, we allow the log asymptotic recruitment of population i to be a linear function of temperature for that population (T_i), i.e.:

$$\log(\alpha_i K_i) = \beta_1 + \beta_2 T_i + f_i$$

where f_i is the random effect with a mean for population i of $\beta_1 + \beta_2 T_i$. The slopes are highly statistically significant (lrt, $p \leq 0.0001$). The statistical significance of estimates from this model are not necessarily easily interpretable, as the test was performed only after we examined the results. Nonetheless, the results are very suggestive. It is interesting to note

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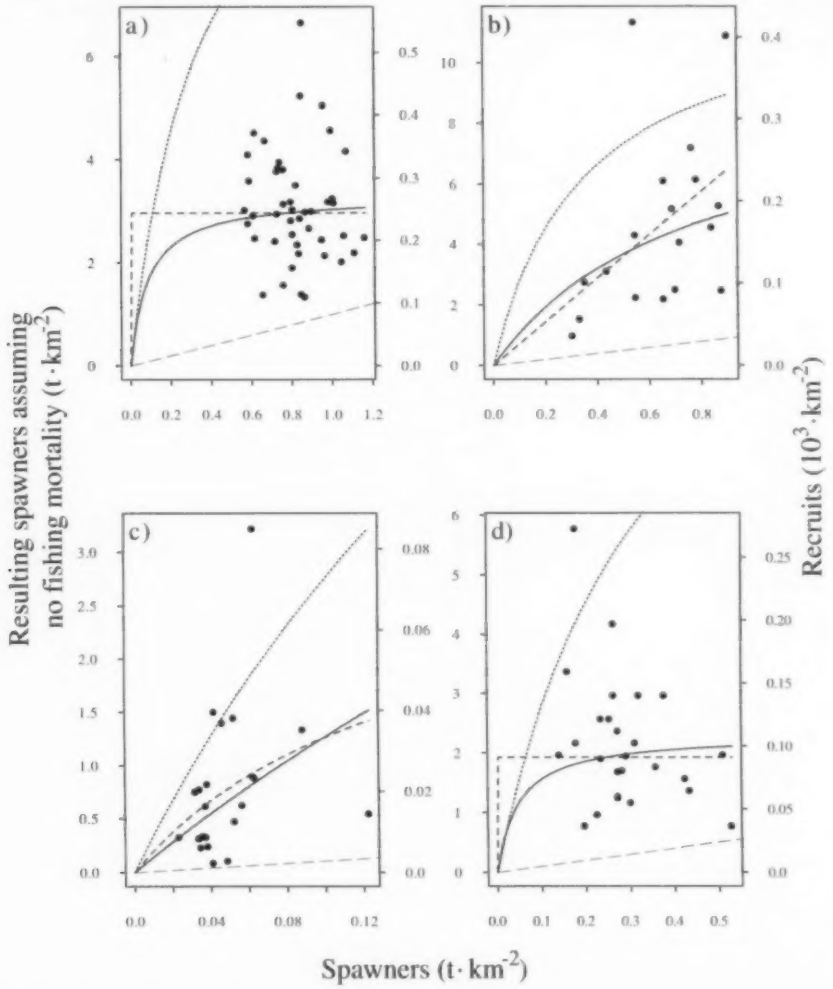
Fig. 2. Spawner–recruit relationships for cod stocks with below-average carrying capacity. (*a*) Southwest Scotian Shelf; (*b*) Georges Bank; (*c*) Celtic Sea; (*d*) west of Scotland. The relationship between recruits per square kilometre and spawning stock biomass per square kilometre for two cod stocks in the Northwest and two cod stocks in the Northeast Atlantic having below-average carrying capacity (empirical Bayes estimated *K* values from the Beverton–Holt model). Note that axis scaling differs among stocks. Solid line: empirical Bayes estimate for the individual stock; curvilinear dashed line: single-stock maximum likelihood fit; dotted line: average estimate for all stocks from the mixed effects model (hence identical in all plots); straight dashed line: 1:1 replacement line.



that the relationship between temperature and asymptotic recruitment is a negative one, i.e., stocks located in warmer waters had lower asymptotic recruitment.

Alternative formulations

An alternative approach to this problem is in the context of generalized linear mixed models. The analysis for a single stock can be modeled by a generalized linear model in which the variation in recruitment is assumed to follow a gamma distribution, and the Beverton–Holt model is modeled as an inverse link (McCullagh and Nelder 1989). If many stocks are considered simultaneously, the parameters $1/\alpha$ and $1/\alpha K$ are assumed to be Gaussian random variables. We implement this approach using the methods of Wolfinger and O'Connell (1993). Unfortunately, the results are not satisfactory because there is no natural way to constrain the parameters α and K to be positive as is required by the model. For the cod stocks, a significant fraction of the estimated K's are negative. Although this approach appears to be attractive — gamma errors may be a more reasonable model — there does not appear to be an easy way to constrain the parameters to be within a reasonable range using present statistical technology unless one uses MCMC methods.

We also carried out a hierarchical Bayes analysis of the same data using MCMC methods implemented in Bayesian inference using Gibbs sampling (BUGS) (Gilks et al. 1994). The results were very similar to the results for the mixed model approach, if all assumptions, i.e., uncorrelated ran-

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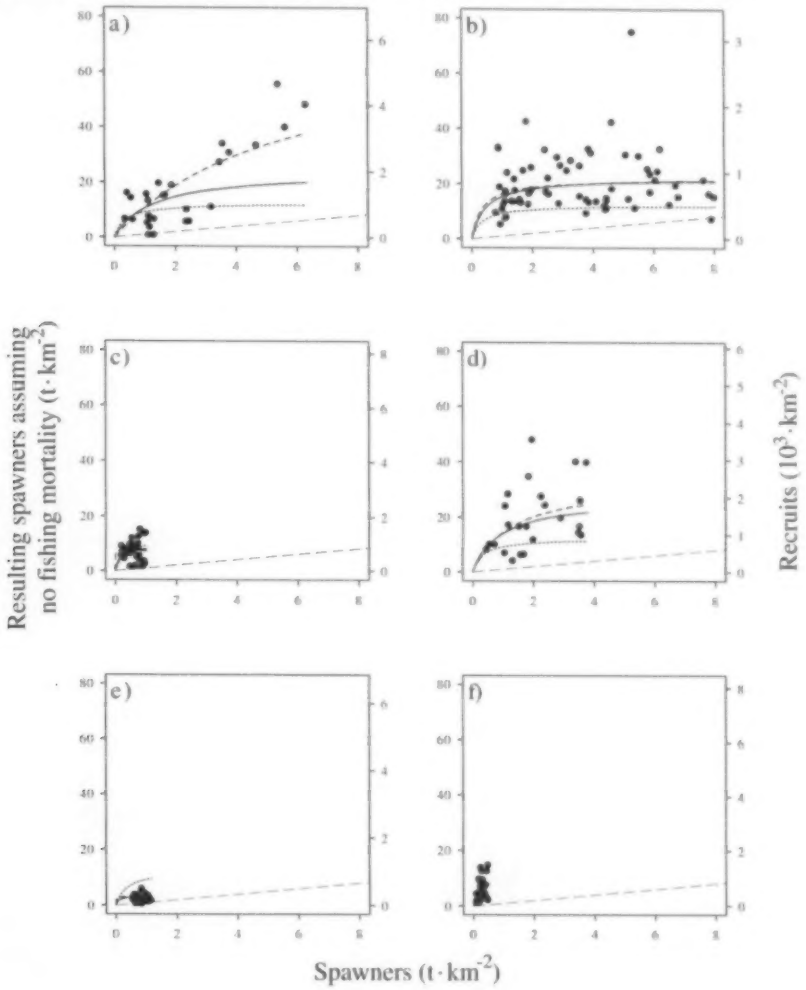
Fig. 3. Relationship between recruits per square kilometre and spawning stock biomass per square kilometre for three cod stocks in the Northwest and three cod stocks in the Northeast Atlantic. (*a*) Labrador and Northeast Newfoundland; (*b*) Iceland; (*c*) Eastern Scotian Shelf; (*d*) Central Baltic; (*e*) Southwest Scotian Shelf; (*f*) North Sea. Note the common scaling on all axes. Solid line: empirical Bayes estimate for the individual stock; curvilinear dashed line: single-stock maximum likelihood fit; dotted line: average estimate for all stocks from the mixed effects model (hence identical in all plots); straight dashed line: 1:1 replacement line.



dom effects and multiple error estimation, remain the same and the priors are uninformative. Thus, we do not provide the results of the analysis here. Finally, the definition of juvenile habitat was restricted to area between 0 and 200 m below sea level. There was no substantial difference in the results for this modification.

Discussion

To our knowledge, this is the first attempt to systematically estimate productivity on a per area basis for this or any other marine fish species. By putting all variables (spawner abundance and recruitment per unit area) and hence parameters (maximum reproductive rate and carrying capacity per unit area) on the same scale, it is possible to address questions that cannot be addressed using traditional methods. We have found evidence that carrying capacity of cod declines at higher temperatures, which, to our knowledge, no one researching cod in the North Atlantic has suspected. It is clear that there is a strong relationship between temperature and somatic growth rate and maximum population growth rate among populations (Brander 1994; Myers et al. 1997), but it is positive, not the negative relationship our analysis suggests. A possible explanation might be the greater number of competitors in warmer water, but this intriguing relationship bears further investigation.

Our main conclusion is that appropriate statistical methods can use information from other studies (stocks) to estimate spawner–recruitment parameters for stocks where these are poorly defined. This has allowed us to identify the re-

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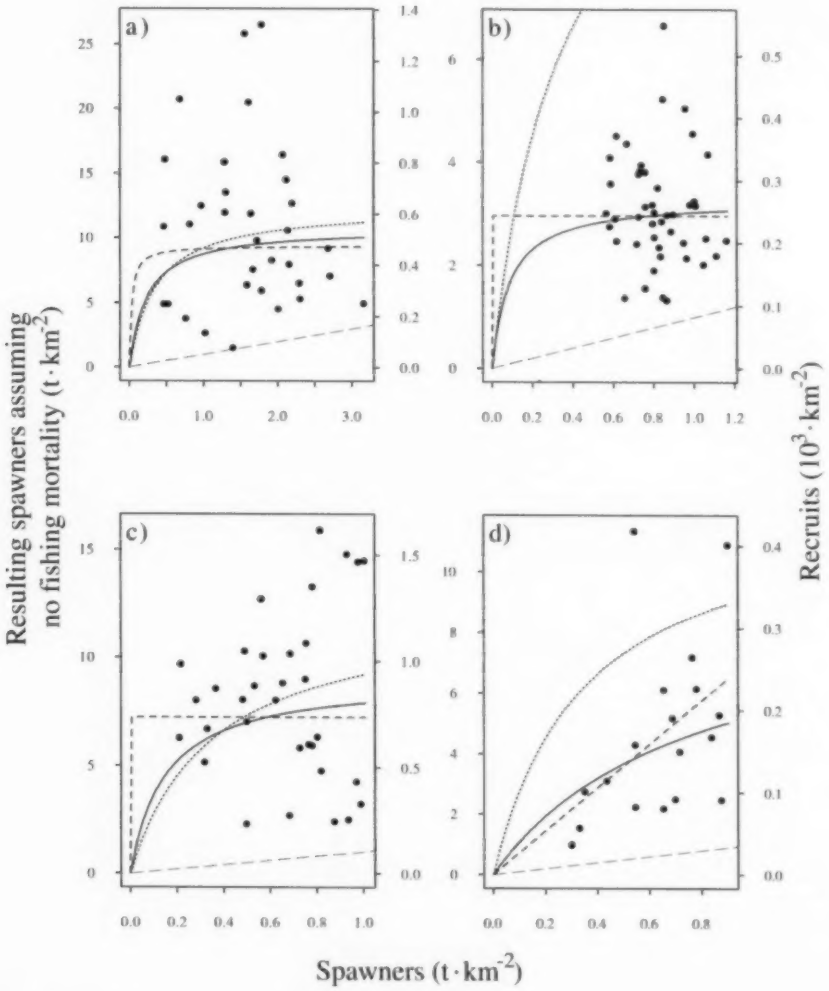
Fig. 4. Relationship between recruits per square kilometre and spawning stock biomass per square kilometre for two cod stocks in the Northwest and two cod stocks in the Northeast Atlantic for which parameter estimation for the Beverton–Holt model on an individual stock basis gave meaningless results (i.e., infinite α or *K*). (*a*) Faroe Plateau; (*b*) Southwest Scotian Shelf; (*c*) Eastern Scotian Shelf; (*d*) Georges Bank. Note that axis scaling differs among stocks. Solid line: empirical Bayes estimate for the individual stock; curvilinear dashed line: single-stock maximum likelihood fit; dotted line: mixed model estimate of species mean; straight dashed line: 1:1 replacement line.



markable variation in carrying capacity per unit area, more than a 20-fold variation, that has previously not been recognized. In the cod example, this method allows spawner–recruitment parameters to be fitted for a given stock even though the data for that stock by itself give implausible estimates. The empirical Bayes estimates are clearly superior in these cases to the individual fits, but it is possible that they may shrink the estimates too close to the mean in some cases. In other words, too much weight may be given to the population estimate for the random effect and not enough weight to the individual-stock estimate. Nonetheless, this finding should be useful when designing management strategies for stocks whose population dynamics are too variable to allow reliable resolution of spawner–recruitment curves. It is also possible to carry out similar analyses on stock production models (see Hoenig et al. (1994) for an excellent example).

A secondary conclusion is that these statistical methods have enabled us to compare carrying capacities and maximum lifetime reproductive rates in different geographic regions occupied by cod stocks. Cod stocks apparently have similar reproductive potentials between areas, but their final long-term mean abundance differs appreciably and is probably related to conditions in the local region. The relative constancy (low variation) of the maximum reproductive rate at low stock sizes that we have estimated is similar to those that have been seen in some previous analyses for cod (Myers et al. 1999).

Our findings based on meta-analytical techniques indicate that there is an approximately 20-fold variation in carrying

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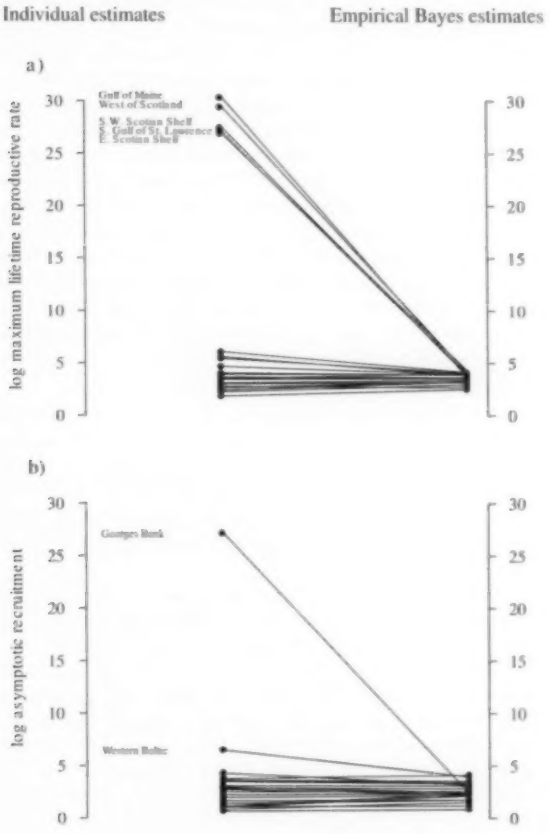
Fig. 5. Comparison of parameter estimates for Beverton–Holt spawner–recruitment curves for 21 cod stocks made on an individual-stock basis or using meta-analytical techniques in a mixed model analysis. Note the large decrease in range of estimated (*a*) α and (*b*) αK for the stocks that gave effectively infinite estimates when estimated individually.

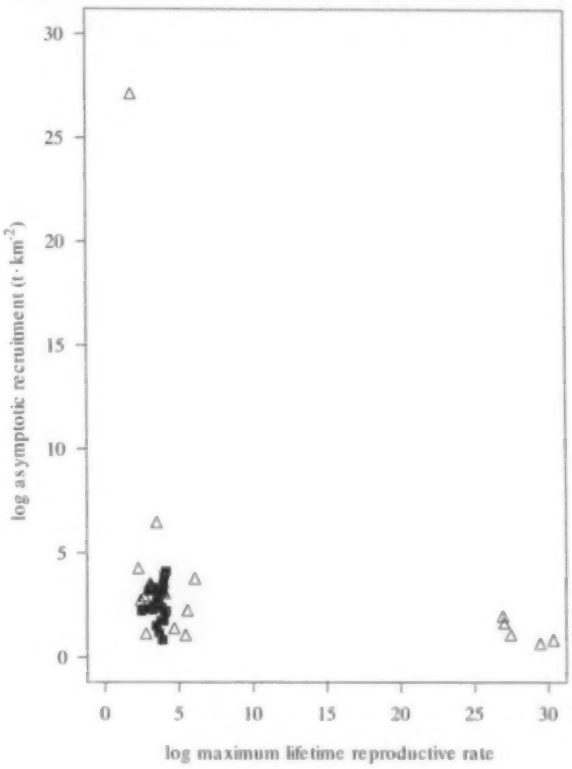


capacity on a per unit area basis among regions. The differences in carrying capacity seem new and we are not aware of similar estimates between stocks, although in a related study, we have observed similarly large differences in recruitment per spawner among stocks of cod and other species (MacKenzie et al. 1999). The exact values for the estimated carrying capacities are approximations because we lack adequate descriptions of habitat area and usage by juvenile cod in all areas and because they ignore the patchy distributions of juvenile cod in nature. The causes for these differences (e.g., rates of plankton and benthic production, habitat quality, abundance of predators and competitors) need to be investigated further.

Understanding the variability among populations and time periods

This analysis provides a way to understand the variability among stocks and time periods. The empirical Bayes estimates yield results that are in all cases reasonable, i.e., no effectively infinite α's or K's, as seen in some of the single-

Fig. 6. Covariation in empirical Bayes estimates (squares) and single-stock maximum likelihood estimates (triangles) of α and αK from the Beverton–Holt stock–recruitment curve for 21 cod stocks.



stock estimates, e.g., Georges Bank and Southwest Scotian Shelf.

In the case where the empirical Bayes estimate of carrying capacity was quite different from the individually fit spawner–recruitment model for the Labrador and Northeast Newfoundland cod stock, this suggests that either the stock is very unusual, the environmental conditions during the period of high recruitment were unusual, the recruitment from that time period was overestimated, or the spawner biomass was underestimated. We believe that the estimates of recruitment and spawner biomass could not be in error sufficiently to cause this discrepancy. The recruitment estimates appear to be valid, as they can be verified by examination of the research surveys carried out at the time (Myers and Pepin 1994). It is unlikely that it is possible that the estimates of spawner biomass could have been in error enough to account for the difference because the recruitment would have been unusual even if the spawner biomass was doubled.

Two possible explanations remain: the habitat area was underestimated before 1966 or the environment was unusual during that period. The first explanation is consistent with clear evidence that the northern component of the stock along the Labrador coast (NAFO Div. 2GH) was fished out and never recovered (Taggart et al. 1994). If this occurred, we would expect the productivity of the stock to appear to be greater than it really is (Ricker 1973). The second explanation is that the environment was fundamentally different.

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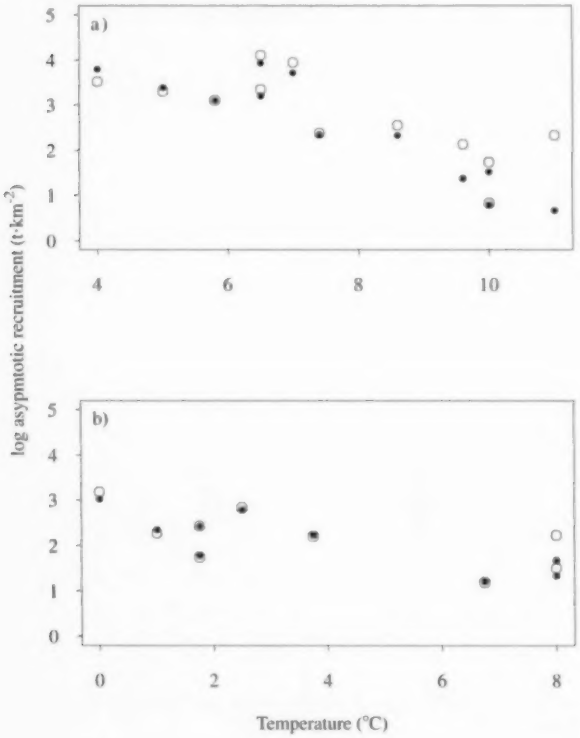
Fig. 7. Relationship between estimated asymptotic recruitment and bottom temperature for each side of the North Atlantic. (*a*) Northeast Atlantic; (*b*) Northwest Atlantic. The estimates of asymptotic recruitment come from two different Beverton–Holt models: one in which asymptotic recruitment is modeled as a linear function of temperature (dots) and one that does not incorporate temperature as a covariate (open circles).



Although sea temperature was warm during the years 1959–1966, attempts to find a link to recruitment for these stocks have led to inconsistent results (Myers 1998). Harp seal (*Phoca groenlandica*) abundance, a potential predator of cod, was declining during the period but was much more abundant than in the 1970s (Stenson et al. 1993). Thus, we believe that it is reasonable to conclude that the Northern cod stock was fundamentally different during the years of high recruitment, either because large substocks were fished out, because of an environmental effect, e.g., unusually warm water, or perhaps because the ecosystem has been fundamentally changed by overfishing (Walters and Kitchell 2001).

Definition of habitat

The area used as habitat will differ among life stages as their requirements change. We have defined juvenile "habitat" as the area of shelf between 0 and 300 m depth, as we believe it is at this stage that habitat area is limiting (Myers and Cadigan 1993). Although our definition is coarse, it is a first step in defining the habitat area and could be extended using other definitions. One difficulty in estimating habitat use now is that we are usually only looking at the remnants of cod populations. In this context, our assumption that all ocean bottom between 0 and 300 m represents juvenile habitat may be inappropriate for detailed comparisons, particularly between stocks whose K differs by relatively small amounts.

No knowledgeable ecologist believes that carrying capacity is constant for any population, as it is certain to change with the environment and the abundance of predators, parasites, and competitors. It is crucial that fisheries ecologists begin developing a predictive understanding of the variability in carrying capacity, as it is central to many ecological and management issues. It is clear that a metaanalytic perspective will be required so as to estimate the variability in carrying capacity both within and between populations. The first step to such an analysis is to standardize carrying capacity on a per unit area basis so that it can be compared across populations. Although many studies have examined the carrying capacity of salmonids per unit area in streams (e.g., Bradford et al. 1997), there have been very few attempts to do the same for marine species (Iles and Sinclair 1982; Rijnsdorp et al. 1992; Hay and McCarter 1997). The approach presented here is a step forward in such analyses.

Multispecies models

One of the prime motivations for this work is to develop statistical approaches to model multispecies interactions in a consistent manner among many ecosystems. This is a question that is of critical concern for cod in the Northwest Atlantic because most populations do not appear to be recovering at a rate that is expected from data for the pre-collapse period (Myers et al. 1997).

Multispecies fisheries models have not, in general, used spawner–recruitment data such as we have discussed to examine variations in carrying capacity with species interactions. There exists a wealth of underutilized data that could be used in this regard but have not been. Taking a meta-analytic approach, perhaps by including species interactions in the type of models considered here, may yield much insight.

Management implications

Recent international and national management regimes rely heavily on the goal of fishing such that the biomass is at or above the level needed to produce maximum sustainable yield. For example, the United Nations Convention of Straddling Fish Stocks and Highly Migratory Fish Stocks requires states that sign the agreement to rebuild stocks to the "biomass that would produce maximum sustainable yield." Similar language exists in the Sustainable Fisheries Act passed by the U.S. Congress. It thus becomes crucial to estimate the biomass level at which maximum yield can be sustained and thus the carrying capacity of ecosystems to produce fish. Traditional methods that rely on oversimplified models that apply to only single stocks of one species usually produce very unreliable and uncertain estimates (Hilborn and Walters 1992). The approach described here allows much improved estimates of average carrying capacity of a stock.

The parameter K can be interpreted as the half-saturation constant, which is the level of spawner abundance at which recruitment is half the maximum. In this context, it is a "threshold" biomass that the spawning biomass should not come close to (Myers et al. 1994). Although there is considerable variability in our estimates, the estimate of K is typi-

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cally around 0.5 $t \cdot km^{-2}$. This suggests that no cod stock should be allowed to approach this low level of spawner abundance. Although this is a useful rough guide, some stocks appear to require a substantially higher spawning biomass per unit area. For example, the Labrador and Northeast Newfoundland stock should have a minimum spawning biomass of around 1.3 $t \cdot km^{-2}$.

Our analysis also provides estimates of the maximum reproductive rate α, which forms the basis of most calculations of management reference points (Mace and Doonan 1988; Hilborn and Walters 1992; Mace 1994). These estimates are certainly far superior to the individual point estimates, but it remains to be seen if they are generally superior to the estimates obtained from a meta-analysis using the Ricker model (Myers et al. 1999). Simulation studies are required to determine this.

For some stocks, relatively little information can be obtained about carrying capacity even with meta-analysis. For example, some stocks are so overexploited that it is very difficult to consider the estimates reliable. If this relationship holds up under further analysis, it would give a very useful guide to the carrying capacity for ecosystems where cod is important.

Acknowledgments

We thank the Natural Sciences and Engineering Research Council of Canada, the Killam Foundation, and the Canadian Foundation for Innovation. Participation by B.R.M. was partly supported by a grant from the European Union FAIR programme (FAIR contract 98-3959, "STORE" project).

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Maternal effects as a recruitment mechanism in Lake Michigan yellow perch (*Perca flavescens*)

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Abstract: Changes that occurred in the distribution of adult Lake Michigan yellow perch (*Perca flavescens*) phenotypic traits suggest that maternal effects on larval traits may be substantially influencing the recruitment of this heavily exploited species. We investigated maternal effects on yellow perch larvae at hatching in 10 maternal lines to test the null hypothesis of no effect of maternal phenotype on offspring phenotype and condition. Analyses lead to a rejection of the null hypothesis and indicated that the observed maternal effects likely resulted from differences among females in size, age, gonadosomatic index, and egg production. The observed maternal effects were expressed in the offspring by differences in larval total length, yolk volume, dry weight, and DNA quantity. Older, larger females were found to have high fecundity, yet low gonadosomatic index. Furthermore, older, larger females produced offspring that were, on average, short with large yolk sacs and high quantities of body reserves, as measured by dry weight and total DNA content. We conclude that the distribution of Lake Michigan yellow perch larval traits at hatching is linked to maternal influences and that this linkage may provide a mechanism through which managers can help rebuild the population.

Résumé : Les changements survenus dans la distribution des caractéristiques phénotypiques des Perchaudes (*Perca flavescens*) adultes du lac Michigan laissent croire que les effets maternels sur les caractéristiques larvaires influencent de façon substantielle le recrutement chez cette espèce fortement exploitée. Nous avons étudié les effets maternels sur des larves néonates de Perchaudes de 10 lignées maternelles dans le but de tester l'hypothèse nulle de l'absence d'effets du phénotype maternel sur le phénotype et la condition de la descendance. Nos analyses nous amènent à rejeter l'hypothèse nulle et indiquent que les effets maternels observés résultent probablement de différences dans la taille, l'âge, l'indice ganadosomatique et la production d'oeufs des femelles. Les effets maternels se manifestent dans la progéniture par des différences dans la longueur totale, le volume du vitellus, la masse sèche et la quantité d'ADN des larves. Les femelles plus âgées et plus grosses ont une forte fécondité, malgré un indice ganadosomatique faible. De plus, ces femelles produisent des petits qui sont, en moyenne, courts avec de gros sacs vitellins et d'importantes réserves corporelles, en masse sèche et en contenu d'ADN total. En conclusion, la distribution des caractère larvaires des Perchaudes du lac Michigan est reliée aux influences maternelles; ces liens peuvent fournir aux gestionnaires un outil qui les aidera à restaurer les populations.

[Traduit par la Rédaction]

Introduction

Recruitment variability is likely attributable to processes in early life history (Houde 1987; Pepin 1989; Leggett and Deblois 1994). The extreme variability in vital rates that characterizes early life stages produces larvae with a wide range of characteristics on which phenotypic selection may act (Rice et al. 1993). Recognition of the potential importance of interindividual variability has led to suggestions that recruitment research may be more successful if it were to focus on individuals rather than on populations (Crowder et al. 1989). For example, many recruitment mechanisms have been found to be size dependent (Miller et al. 1988). Because of this size dependence, small initial size differences within a population can result in very large survival and recruitment differences (Adams and DeAngelis 1987; Crowder et al. 1989; Rice et al. 1993).

Previous research has linked observed variation in the early life history traits among individuals of many finfish species to maternal influences (Chambers and Leggett 1992, 1996). Maternal effects can be defined as comprising "a class of phenotypic effects that parents have on phenotypes of their

Received November 28, 2000. Accepted May 9, 2001. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on June 21, 2001.
J16102

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 DOI: 10.1139/cjfas-58-7-1477 © 2001 NRC Canada

offspring that are unrelated to the offspring's own genotype" (Bernardo 1996). Maternal influences result from differential reproductive investment by males and females. The female's energetic investment provides the nutritional requirements essential for proper development and survival until first feeding. These investments by the female can be measured by the morphological and biochemical condition of the offspring. In contrast, paternal investment and its impact on subsequent survival are believed to be small. Recent research on parental influences in Atlantic cod (*Gadus morhua*) did not show any consistent effects of male size on fertilization success (Rakitin et al. 1999). Furthermore, Rakitin et al. (1999) found that differences in hatching success and survival in Atlantic cod could not be explained by differences in male size or sperm density.

Much of the previous research on maternal effects has focused on detecting maternal effects in the phenotypic traits of eggs. Significant female effects on egg size have been observed in many freshwater, marine, and anadromous species (e.g., Hislop 1988; Chambers and Leggett 1996; Chambers and Waiwood 1996). In contrast, research on maternal effects on the size, condition, and growth rates of larvae has been limited (Benoît and Pepin 1999). Significant maternal effects in larval traits have been observed in a few species. The traits for which these effects have been documented are size at hatch (chum salmon (*Oncorhynchus keta*), Beacham and Murray 1985; Atlantic silverside (*Menidia menidia*), Bengston et al. 1987), yolk volume at hatch (chum salmon, Beacham and Murray 1985; capelin (*Mallotus villosus*), Chambers et al. 1989), and size at metamorphosis (winter flounder (*Pleuronectes americanus*), Chambers and Leggett 1992). Chambers and Leggett (1996) concluded that "body size during larval life was likely to be significantly influenced by maternal effects." For most other species where significant maternal effects have been reported in larval traits, such correlations have been extrapolated from significant maternal effects in phenotypic egg traits, which may be inappropriate (Pepin and Miller 1993; Benoît and Pepin 1999).

Maternal effects have the potential to substantially impact the recruitment dynamics of heavily exploited populations. Changes in the distributions of size, age, and condition of the spawning population that result from exploitation can potentially cause changes in egg production, fertilization success, and hatching success (Rijnsdorp 1989). Furthermore, changes in the size and condition distribution of newly hatched offspring of a population can potentially lead to changes in their susceptibilities to starvation and predation. In theory, such shifts can result in increased mortality, decreased recruitment, and ultimately recruitment failure.

An ideal model for research on the influence of maternal effects on recruitment is yellow perch (*Perca flavescens*). Historically, yellow perch has supported one of the most important commercial and recreational fisheries in Lake Michigan (Francis et al. 1996). However, the population has experienced nearly constant recruitment failure since 1990. In 1998, the yellow perch population level was reported to be 20% of 1990 levels (Pradeep Hirethota, Wisconsin Department of Natural Resources Fish Unit (WDNRFU), 600 E. Greenfield Ave., Milwaukee, WI 53204, U.S.A., unpublished data). In addition to declines in abundance, the age structure of the population changed over this period as well (Francis et al. 1996). In the mid- and late 1980s, the population was dominated by yellow perch 2–4 years of age, with a relatively small portion of the total population exceeding 4 years of age. By 1994, the population had shifted to one composed of almost exclusively greater than 4-year-old yellow perch. Furthermore, there are very few yellow perch remaining in the population that are greater than 7 years of age (Pradeep Hirethota, WDNRFU, Milwaukee, WI 53204, U.S.A., unpublished data). In response to the population decline, the average growth rates of female yellow perch have increased substantially since 1983 (Shroyer and McComish 1999). In the early and mid-1980s, female yellow perch reached a size of about 250 mm at an age of 12 years, while in the mid-1990s, females were reaching that same size at an age of only 4 years.

The changes in the population structure that have occurred over the past decade reflect the impact of an extremely size-selective fishery, which targeted the larger female yellow perch. It is likely that the high fishing mortality rate, the highly size-selective nature of the fishery, and a lack of recruitment caused the overall population decline and shifts in the population sex ratio, which have further weakened reproduction and recruitment. The changes in the female portion of the Lake Michigan yellow perch population structure suggest that the distribution of female phenotypes has been significantly altered. Large females that are predominantly greater than 4 years of age, but that are historically young for their size, dominate the female portion of the population (Shroyer and McComish 1999). The lack of recruitment further fuels this phenotypic bottleneck. These changes suggest that maternal effects may now play a dominant role in the recruitment dynamics of yellow perch in Lake Michigan.

Here, we investigate the role of maternal effects within the Lake Michigan yellow perch population. The objectives of this study were threefold: to determine whether maternal effects on larvae of Lake Michigan yellow perch were present, to determine which larval traits accounted for any detected maternal effects, and to determine which female traits correlate with the larval traits that account for any observed maternal effects.

Materials and methods

We investigated our objectives within a single experiment, which involved quantifying the relationship between 10 different females and their offspring at hatching. Additional objectives were investigated within a continuation of this experiment out to 32 days posthatch; however, those results will be examined elsewhere. All females for this experiment were collected in Lake Michigan. Subsequent experimental work was conducted at the University of Wisconsin's WATER Institute, Milwaukee, Wis. The experiment was conducted as a randomized complete block design consisting of three blocks of 20 tanks with two replicate tanks per female per block.

Collection of parental brood stock and gametes

Yellow perch were collected in June 1998 off Green Can Reef (42°50′00″ N, 87°50′00″ W), a historic yellow perch spawning ground offshore of Milwaukee. Fish were collected in bottom-set, graded-mesh gill nets (mesh from 5.7 to 6.4 cm bar) fished overnight. Female yellow perch were determined to be green (not ready to spawn, eggs not fully hydrated), ripe (eggs fully hydrated and

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Table 1. Maternal and larval traits measured in each of the yellow perch females and sampled offspring of the 10 maternal lines.

Maternal trait	Larval trait
Linear measures	
Total length (mm)	Total length (mm)
Weight (g)	Eye diameter (mm)
Body depth at the anterior base of the first dorsal fin (FBD_1) (mm)	Minor yolk axis (mm)
Body depth at the posterior base of the second dorsal fin (FBD_2) (mm)	Major yolk axis (mm)
Age (years)	Body depth at insertion point of the pectoral fin (BDIP) (mm)
Egg production (no.)	Body depth at insertion point of the first dorsal fin (BDID) (mm)
	Body depth at insertion point of the anus (BDIA) (mm)
Biochemical measures	
	RNA content (RNA) (μg)
	DNA content (DNA) (μg)
Derived measures	
Fulton's condition factor k ($g \cdot mm^{-3}$)	Yolk volume (mm^3)
GSI	Dry weight (mg)
	RNA:DNA

easily expressed), or spent. Eggs of ripe female yellow perch were immediately expressed, weighed, and then fertilized with the milt from no fewer than three and no more than eight ripe males. Fertilized egg skeins were kept separate and transported back to the laboratory in Ziploc bags. The adult females and males used to produce each fertilized egg skein were killed and kept in separate bags on ice for transportation back to the laboratory. Egg skeins from five female yellow perch were obtained on 2 June 1998; five additional egg skeins were obtained on 4 June 1998.

Determination of maternal characteristics

We quantified eight maternal traits (Table 1). The total length and weight of each female were measured in the laboratory. Fulton's condition factor (k) was calculated for each female as $k = (\text{weight}/\text{length}^3) \times 100\,000$. Additionally, the body depths at the anterior base of the first dorsal fin and the posterior base of the second dorsal fin were measured. The sagital otoliths of each female were removed for age analysis. Each female's gonadosomatic index (GSI) was determined as

$$(1) \quad GSI = \frac{\text{wet wt. eggs} + \text{wet wt. stripped ovary}}{\text{wet wt. stripped female} + \text{wet wt. eggs} + \text{wet wt. stripped ovary}}$$

When the ovary from each female was removed, there were some green eggs remaining in each ovary. These eggs were determined to be eggs that would not have been released during spawning and would most likely have been reabsorbed by the female; therefore, our estimates of total egg production for each female are based solely on the ripe eggs expressed. Since the green eggs remaining in the ovary were assumed to be eggs that would have been reabsorbed, their weight was included in the weight of the stripped ovary.

Egg sampling

The total volume of each female's egg skein was measured in the laboratory. Independent 1-mL subsamples ($n = 3$) of each egg skein were taken and the eggs in each subsample were enumerated. The total egg production per female was defined as the product of the skein volume and the average egg concentration per unit volume. An additional subsample of each female's eggs was videotaped for subsequent analysis of morphometry ($n = 15$). For unknown reasons, the gelatinous matrix of Female 2 did not hold together. While we were able to get egg production estimates for Female 2, we did not videotape her eggs to avoid risking loss of too many eggs.

Husbandry of eggs

Once egg skeins from 10 females were available, the eggs were randomly assigned to, and incubated in, flow-through, temperature-controlled 10-gal (US) aquaria. Based upon the previously determined number of eggs per millilitre (checked again on 4 June 1998 to adjust for swelling associated with water hardening), a volume of skein equivalent to 2000 eggs was placed into each tank assigned to that female. The egg skein for Female 5 was crushed in transport and some eggs were damaged; the total number of usable eggs for Female 5 was only 1400 per tank.

Hatching began on 14 June 1998 in all tanks. Hatching was encouraged by gently mixing the water and the broken egg skeins to allow those larvae trapped within the gelatinous matrices to be freed. The broken egg skeins and any dead eggs and larvae were removed.

Larval sampling

We sampled 15 larvae at hatch from each tank, resulting in a total of 90 larvae per female. The larvae were anesthetized with tricaine methansulfonate (MS 222) and videotaped for analysis of morphometry. We sampled 12 larval traits, of which nine were morphometric measures and three were biochemical measures of condition (Table 1). The individual larvae were then placed into cryovials and flash-frozen in liquid nitrogen and then stored at –80°C for subsequent extraction of nucleic acids. There was a loss of a portion of videotape record for each female due to a problem with the video recording device that was not evident until analysis of the videotape began. Therefore, means of individual larval traits are based upon variable sample sizes ranging from 67 to 81 larvae per female.

Postsampling processing of eggs and larvae

Analysis of morphometric landmarks of the eggs and larvae from videotaped images was conducted with an image analysis system at the Chesapeake Biological Laboratory in Solomons, Md. The two-dimensional surface area and three sides of a triangle inscribed within the outline of each female's individual eggs and egg yolks were measured. Total egg volume and egg yolk volume were then determined based upon the following equations adapted from Miller et al. (1995):

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Table 2. Phenotypic characteristics of the 10 female yellow perch caught off Green Can Reef (42°50′00″N, 87°50′00″W), Lake Michigan.

Female	Total length (mm)	Weight (g)	Fulton's condition factor k	Age (years)	FBD_1 (mm)	FBD_2 (mm)	GSI	Egg production (no.)
1	250	145.3	0.9299	4	53	47	0.3589	22 600
2	227	124.7	1.066	4	46	44	0.6284	11 000
3	280	255.6	1.164	4	72	57	0.5676	36 100
4	249	151.3	0.9802	2	54	43	0.6170	23 600
5	256	169.9	1.013	3	55	46	0.3824	11 600
6	285	261.4	1.292	5	65	61	0.2869	36 700
7	287	255.7	1.082	6	65	62	0.2168	29 400
8	216	113.1	1.122	3	47	40	0.4064	30 600
9	222	115.7	1.058	3	45	41	0.2875	22 000
10	242	115.4	0.8145	4	49	46	0.3989	32 800

Note: Females 1–5 were collected on 2 June 1998 and Females 6–10 were collected on 4 June 1998. Trait abbreviations are as defined in Table 1.

$$(2)\quad \text{Volume}(\text{mm}^3) = \frac{4}{3}\pi R^3$$

$$(3)\quad R = \frac{abc}{4K}$$

$$K = \sqrt{s(s-a)(s-b)(s-c)}$$

$$s = \frac{a+b+c}{2}$$

where R is the estimated radius of the sphere and a, b, and c represent the three triangle sides inscribed within each egg and egg yolk.

Total length, eye diameter, body depth at the insertion point of the pectoral fin, body depth at the insertion point of the first dorsal fin (inclusive of the yolk sac), and body depth at the insertion point of the anus were measured for each individual larva sampled. The two-dimensional surface area of each larva's yolk sac was measured along with the major and minor yolk axes. Total yolk sac volume was then estimated as

$$(4)\quad \text{Volume } (\text{mm}^3) = \frac{4}{3}(\text{length of the minor yolk axis} \times \text{yolk surface area})$$

The two-dimensional body area of each larva was also measured, and a calibration from other newly hatched yellow perch larvae between two-dimensional body area (square millimetres) and dry weight (milligrams) allowed estimation of individual larval dry weight (dry weight = $[(2 \times 10^{-6}) \times (\text{body area})^2 + (6 \times 10^{-5}) \times (\text{body area}) + (3 \times 10^{-5})] \times 1000$, $n = 171$, $r^2 = 0.9836$, $p = 0.0001$).

Nucleic acids were extracted from each individual larva by a modification of the sarcosyl extraction technique described by Caldarone and Buckley (1991). Whole frozen larvae were placed in individual microcentrifuge tubes containing 150 µL of 1% sarcosyl solution (*N*-lauroylsarcosine: Sigma L-5125). After vortexing for 1 h, 1.35 mL of Tris buffer (5 mM Tris–HCl (Trizma base: Sigma T-8524, HCl: Sigma H-1758), 0.5 mM EDTA (Sigma E-5134), pH 7.5) was added to reduce the sarcosyl concentration to 0.1%, and the tubes were centrifuged at 14 000 × *g* for 15 min to sediment any remaining tissue structures. Nucleic acids were quantified with a fluorometric technique described by Wagner et al. (1998). Seventy-five-microlitre aliquots of the supernatant from each microtube were combined with 75 µL of ethidium bromide (ISC Bioexpress C-5515-10) in 96-well microplates. A dilution series of 18s, 28s calf liver rRNA (Sigma R-0889) and calf thymus DNA (Sigma D-4764) standards, blanks of 0.1% sarcosyl, and an extracted 9 days posthatch yellow perch homogenate control were also combined with ethidium bromide (75 µL : 75 µL) on each plate. After shaking for 15 min, the microplate was scanned on a fluorescence plate reader (Ex = 545 nm, Em = 575 nm, bandwidth = 9 nm) (IDEXX FCA-VIP, IDEXX Corp., Portland, Me.) to determine total nucleic acid fluorescence in each sample. A volume of 7.5 µL of RNase A (Sigma R-6513) was then added to each well of the microplate. The plate was shaken for 20 min to digest the RNA in each sample and scanned a second time to determine the quantity of DNA in each sample. The fluorescence remaining after the addition of RNase was attributed to DNA only after verification that the addition of DNase yielded background fluorescence values similar to the 0.1% sarcosyl blanks. The fluorescence due to RNA was calculated from the difference in fluorescence between total nucleic acid values and DNA values for each sample. The concentrations of RNA and DNA in each sample were determined from the standard calibration curves run with each plate, and the ratio of total RNA to total DNA (RNA:DNA) in each sample was calculated. To reduce error associated with any one day's reading, only a few of the larvae from an individual tank were read on a given day.

Statistics

Separate statistical analyses were conducted to address our three objectives. All statistical analyses were conducted using SAS software version 6.12 (SAS Institute Inc. 1996). We used 12 larval and eight maternal traits in our analyses (Table 1). The presence of significant maternal effects at hatching in the offspring of the 10 females was determined by multivariate analysis of variance (MANOVA, SAS, Proc GLM) on all larval traits at hatching. The MANOVA was based upon the mean value of each larval trait within each tank for each female nested within her date of fertilization (2 June or 4 June 1998). Significance of MANOVA was determined based upon a Wilks λ statistic with 96 and 259.507 degrees of freedom.

The larval traits that accounted for the observed maternal effects at hatch were determined by univariate analysis of variance (ANOVA, SAS, Proc Mixed) on biologically important larval traits within each tank for each female nested within her date of fertilization. Significance of each ANOVA was determined based upon an F statistic with 8 and 48 degrees of freedom.

To determine which female traits correlated with the larval traits that accounted for the observed maternal effects at hatch, we performed a canonical correlation analysis on the female and larval data (SAS, Proc Cancorr). Significance of the overall canonical

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Table 3. Mean initial number of eggs (±SD) in each female's replicate tank (n = 6), mean number of offspring at hatching (±SD), and percent hatching success in the 10 yellow perch maternal lines.

Female	Mean initial number of eggs (n = 3)	Mean initial number of offspring (hatching success) (n = 6)	Hatching success (%)
1	2002±14	1615±289	80.7
2	1968±11	89±20	4.5
3	2000±18	896±181	44.8
4	2024±15	1538±133	76.0
5	1392±12	1148±198	82.5
6	2040±12	1269±228	62.2
7	2020±11	1610±290	79.7
8	2002±6	1061±381	53.0
9	2032±14	1379±164	67.9
10	1965±17	1287±188	65.5

correlation analysis was based upon a Wilks λ statistic with 80 and 274.95 degrees of freedom. We report the trait loadings on significant canonical correlation axes only.

Results

The females had a wide distribution of phenotypic traits. Female total length ranged from 216 to 287 mm and female weight ranged from 113 to 261 g. Females ranged in age from 2 to 6 years. GSI ranged from 0.22 to 0.63, while egg production ranged from 11 400 to 36 720 eggs (Table 2). Correlation analysis indicated that female total length, weight, Fulton's condition factor k, body depth, age, and egg production were all positively correlated with one another and negatively correlated with GSI.

Mean hatching success of the eggs was highly variable among the 10 maternal lines. The lowest mean number of offspring observed was for Female 2, representing 4.5% hatching success. Excluding Female 2, given the poor quality of her egg skein, the range of hatching success varied from 44.8% hatching success for Female 3 to 82.5% for Female 5 (Table 3).

Means (±SD) for each trait are provided (Table 4). Mean larval total length ranged from 5.5 ± 0.43 mm (Female 9) to 6.2 ± 0.39 mm (Female 2). Mean eye diameter varied the least among all females. Female 3 had the lowest mean yolk volume, 0.04 ± 0.012 mm^3, while Female 7 exhibited the highest, 0.07 ± 0.017 mm^3. Mean body depth at the insertion point of the pectoral fin ranged from 0.65 ± 0.081 mm (Female 9) to 0.73 ± 0.088 mm (Female 4), mean body depth at the insertion point of the first dorsal fin ranged between 0.63 ± 0.087 mm (Female 1) and 0.8 ± 0.11 mm (Female 7), and mean body depth at the insertion point of the anus ranged from 0.51 ± 0.078 mm (Female 8) to 0.59 ± 0.079 mm (Female 4). Mean dry weight ranged from 0.19 ± 0.016 mg (Female 9) to 0.24 ± 0.024 mg (Female 7). Mean RNA ranged from 2.7 ± 0.63 µg (Female 9) to 3.8 ± 0.55 µg (Female 7), while DNA ranged from 1.7 ± 0.21 µg (Female 9) to 2.3 ± 0.30 µg (Female 7) between the hatchlings. Despite relatively large differences in the mean quantity of RNA and DNA in the larvae, the mean RNA:DNA only varied between 1.5 ± 0.32 (Female 5) and

Table 4. Mean phenotypic characteristics (±SD) of the yellow perch offspring of the 10 maternal lines sampled at hatching on 14 June 1998.

Female	n	Mean total length (mm)	Mean eye diameter (mm)	Mean yolk sac volume (mm^3)	Mean BDIP (mm)	Mean BDID (mm)	Mean BDIA (mm)	Mean dry weight (mg)	Mean RNA (µg)	Mean DNA (µg)	Mean RNA:DNA
1	80	6.1±0.47	0.38±0.044	0.05±0.015	0.7±0.091	0.63±0.087	0.56±0.083	0.22±0.023	3.4±0.98	2.1±0.34	1.7±0.69
2	70	6.2±0.39	0.39±0.042	0.04±0.014	0.68±0.093	0.64±0.094	0.54±0.021	0.22±0.019	3.2±0.93	2.2±0.30	1.5±0.45
3	78	6.1±0.47	0.39±0.05	0.04±0.012	0.68±0.086	0.66±0.091	0.55±0.087	0.22±0.022	3.4±0.5	2.1±0.37	1.7±0.47
4	81	6.2±0.46	0.38±0.044	0.05±0.015	0.73±0.088	0.67±0.083	0.59±0.079	0.23±0.022	3.4±0.66	2.2±0.29	1.6±0.43
5	76	6.1±0.44	0.39±0.043	0.05±0.015	0.69±0.086	0.64±0.087	0.56±0.081	0.22±0.017	3.2±0.6	2.1±0.25	1.5±0.32
6	77	5.5±0.48	0.42±0.047	0.06±0.012	0.67±0.087	0.75±0.085	0.53±0.069	0.20±0.018	3±0.61	1.9±0.31	1.6±0.71
7	67	6.1±0.41	0.39±0.045	0.07±0.017	0.72±0.077	0.8±0.11	0.57±0.088	0.24±0.024	3.8±0.55	2.3±0.30	1.6±0.29
8	75	5.6±0.4	0.38±0.048	0.06±0.015	0.69±0.091	0.8±0.14	0.51±0.078	0.2±0.019	2.9±0.68	1.8±0.38	1.7±0.67
9	70	5.5±0.43	0.35±0.04	0.05±0.011	0.65±0.081	0.73±0.096	0.51±0.075	0.19±0.016	2.7±0.63	1.7±0.21	1.6±0.41
10	78	5.7±0.42	0.42±0.036	0.07±0.014	0.69±0.096	0.76±0.112	0.51±0.081	0.21±0.018	3.3±0.53	1.9±0.42	1.8±0.78

Note: Trait abbreviations are as defined in Table 1.

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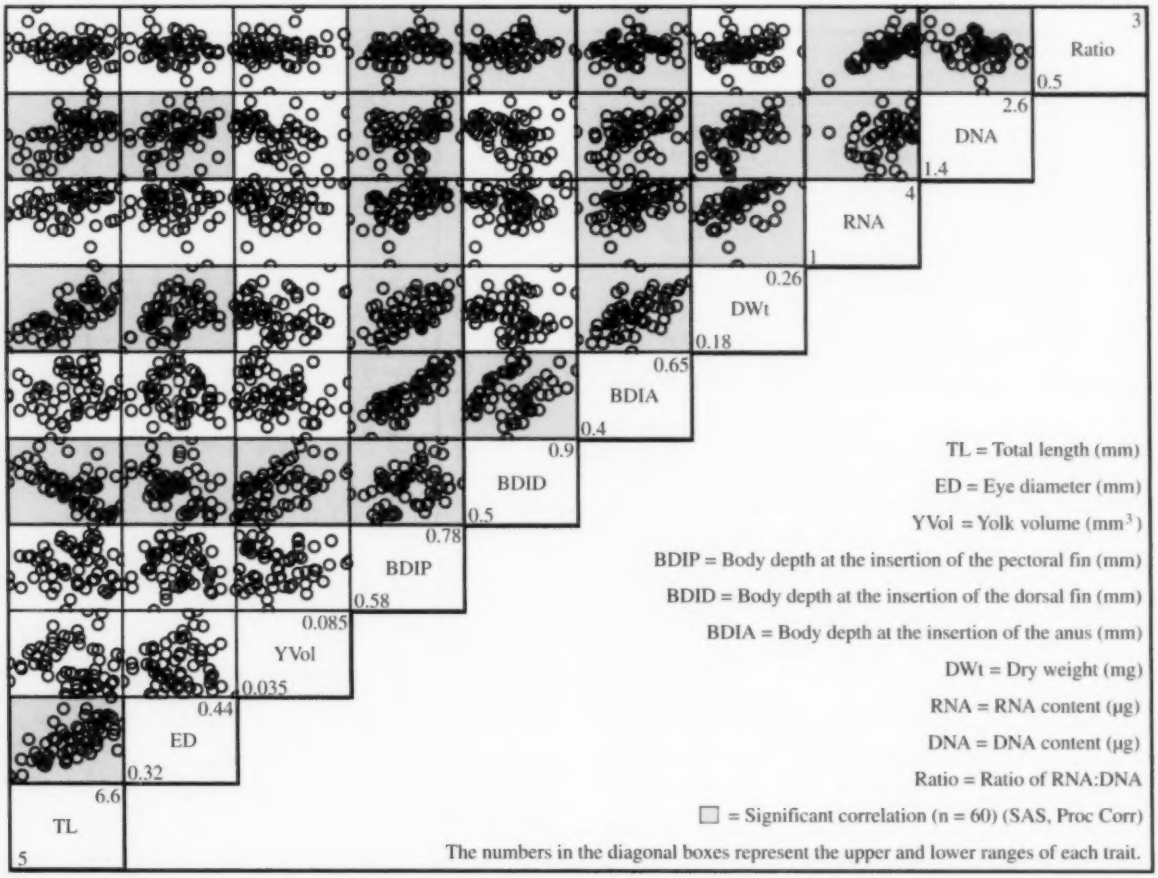
Fig. 1. Bivariate correlations among 10 larval traits of yellow perch. Data plotted are mean values of each trait based on analysis of between 67 and 81 larvae in each of 60 tanks that comprised the experiment.



1.8 ± 0.78 (Female 10) among the offspring of the 10 maternal lines.

Correlation analysis of tank mean values for 10 larval traits showed a highly variable covariance structure (Fig. 1). Some trait pairs were highly correlated (e.g., larval body depth at the insertion of the pectoral fin and larval body depth at the insertion of the anus (r = 0.8297, n = 60, p = 0.0001), larval total length and larval dry weight (r = 0.7093, n = 60, p = 0.0001), and RNA and RNA:DNA (r = 0.7406, n = 60, p = 0.0001)). Both negative and positive correlations were present in the morphometric data (Fig. 1). However, other trait pairs exhibited no significant correlation (e.g., larval total length and larval yolk volume (r = –0.1309, n = 60, p = 0.3188) and larval yolk volume and larval dry weight (r = 0.0527, n = 60, p = 0.6893)). Nucleic acid based traits showed strong correlations internally. However, with the exception of a correlation between DNA and larval dry weight, there were only weak correlations between nucleic acid based traits and morphometric traits.

We were able to reject the null hypothesis of no overall maternal effect among the offspring of the 10 maternal lines for larval traits based upon MANOVA results ($F_{96,\ 259.507}$ = 2.21, p = 0.0001). Univariate ANOVAs indicated an overall significant difference between the offspring of the 10 maternal lines for larval total length, larval yolk volume, larval dry weight, and DNA (Table 5; Fig. 2).

There was a significant canonical correlation between the maternal and larval traits ($F_{80,\ 274.95}$ = 4.51, p = 0.0001). The canonical correlation analysis indicated that canonical correlation axes I, II, and III were the only significant correlations, with canonical correlation axis I explaining 54% of the variance, canonical correlation axis II explaining 33.6%, and canonical correlation axis III explaining 5.5% of the variance. Because canonical correlation axis III explained only 5.5% of the variance, we did not consider it further. The female traits age, GSI, and egg production were strongly associated with the Female I canonical correlation. Female age and egg production were weighted negatively on canonical correlation Female I, while GSI was weighted positively (Table 6). The canonical correlation Female II was a strong positive descriptor of female size and age (Table 6). The larval traits larval total length, larval yolk volume, and larval body depth at the insertion of the first dorsal fin were strongly associated with the Larval I canonical correlation. Larval total length was weighted positively on canonical correlation Larval I, while larval yolk volume and larval body depth at the insertion of the first dorsal fin were weighted negatively on the axis (Table 7). The canonical correlation

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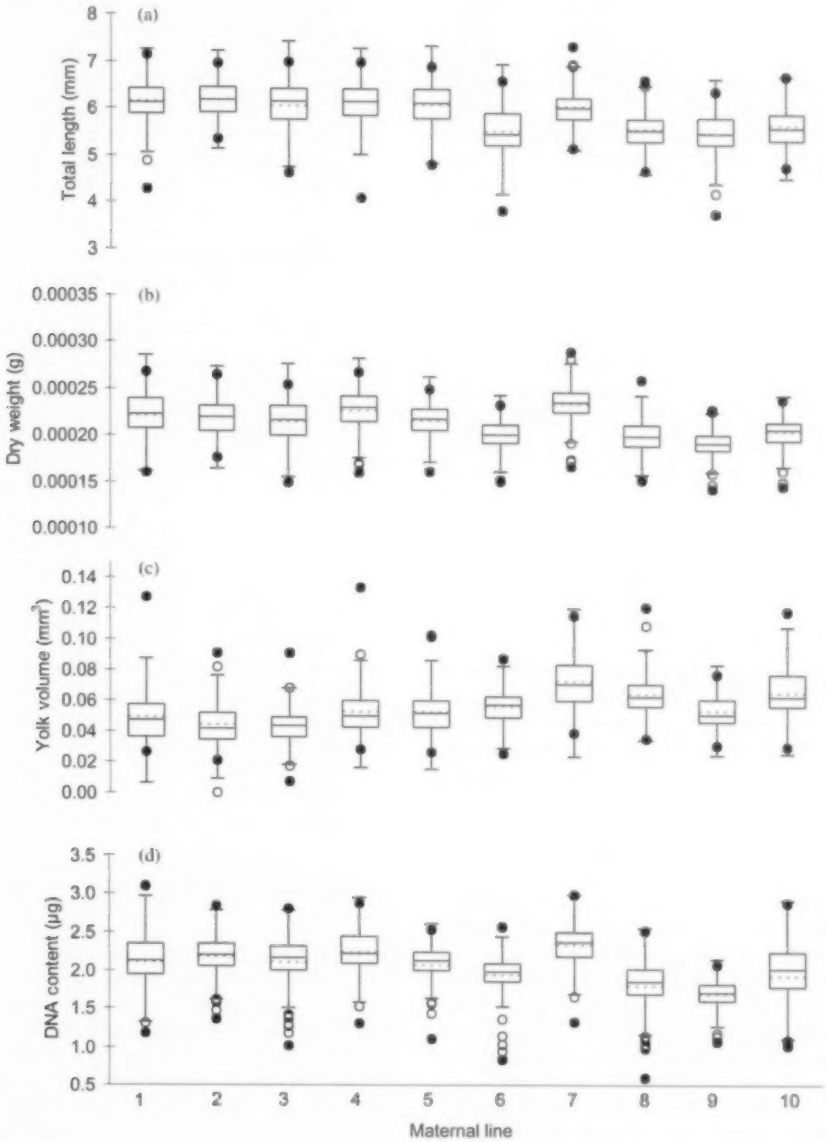
Fig. 2. Box and whiskers plot of (*a*) total length, (*b*) dry weight, (*c*) yolk sac volume, and (*d*) DNA content of yellow perch offspring from 10 maternal lines at hatching. The upper and lower limits of the box represent the third (Q_3) and first (Q_1) quartiles, respectively. The solid horizontal line within the box represents the median value of the data. The dashed horizontal line within the box represents the mean value of the data. The upper and lower extremes of the whiskers represent ($Q_3 + 1.5(Q_3 - Q_1)$) and ($Q_1 - 1.5(Q_3 - Q_1)$), respectively. Data outside the whiskers are considered outliers and are represented by open circles. Solid circles represent the minimum and maximum values of the data.



Larval II was a strong positive descriptor of larval size and nucleic acid content (Table 7).

Furthermore, 54% of the variation that we observed among the larvae of the 10 maternal lines was explained most by differences in larval total length, larval yolk volume, and larval body depth at the insertion of the first dorsal fin and was associated most with differences in female GSI, egg production, and age (Table 8). An additional 33.6% of the variation among the larvae of the 10 maternal lines was expressed most in larval size (particularly larval dry weight) and nucleic acid content and was most associated with differences in female size and age (Table 8).

Discussion

We detected significant maternal effects at hatch among the offspring of the 10 yellow perch females. Analyses indicate that these effects likely result from differences among

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Table 5. Univariate ANOVA results for tests of significant yellow perch maternal effects, for individual larval traits, among the offspring of the 10 maternal lines (n = 752).

Larval trait	AIC	F	Pr > F
Mean total length	7.41	5.86	0.0001
Mean eye diameter	75.80	0.55	0.81
Mean yolk volume	199.12	3.45	0.0032
Mean BDIP	104.28	1.69	0.12
Mean BDID	98.11	2.04	0.062
Mean BDIA	103.48	1.62	0.14
Mean dry weight	178.72	10.78	0.0001
Mean RNA	–49.65	1.68	0.13
Mean DNA	18.14	7.31	0.0001
Mean RNA:DNA	–17.74	0.00	1.0

Note: Trait abbreviations are as defined in Table 1. Univariate tests were performed with 8 and 48 degrees of freedom. AIC, Akaike's information criterion.

Table 6. Canonical correlation analysis: female loading results for the eight female phenotypic traits of the 10 female yellow perch.

	Canonical correlation	
Female trait	Female I	Female II
Total length	0.0140	0.5477
Weight	–0.0476	0.4185
Fulton's condition factor k	–0.0474	–0.1657
Age	–0.4114	0.4898
GSI	0.6980	–0.0551
Egg production	–0.5160	0.0808
FBD_1	0.0800	0.4096
FBD_2	–0.1976	0.4985

Note: Trait abbreviations are as defined in Table 1.

females in size, age, GSI, and egg production. Furthermore, larvae expressed the maternal effects by differences in larval total length, larval yolk volume, larval dry weight, and DNA quantity. However, we found no significant differences in egg volume or egg yolk volume among the eggs from the different females.

Previous research on maternal effects has focused largely on correlations between the phenotypic traits of the female and the phenotypic traits of her eggs. There has been substantially less focus on the relationship between female phenotypic traits and the phenotypic traits of her offspring, both immediately following hatching and throughout the larval stage. This focus is perhaps driven by the need of fisheries scientists to predict recruitment as early as possible in the fish's ontogeny and by the underlying hypotheses that egg size is predictive of larval size and subsequent performance (see reviews by Chambers and Leggett 1996; Chambers and Waiwood 1996). Also, propagule size is an obvious expression of maternal effects that should correlate with the female's phenotype (Bernardo 1996; Solemdal 1997). In light of this, our failure to detect maternal effects in egg volume or egg yolk volume of yellow perch is surprising. The most likely explanation for the absence of a relationship between either egg volume or egg yolk volume and maternal phenotype or larval phenotype is the reproductive style of yellow perch. Yellow perch females release an egg skein in

Table 7. Canonical correlation analysis: larval loading results for the 10 larval phenotypic traits from the 10 yellow perch maternal lines.

	Canonical correlation	
Larval trait	Larval I	Larval II
Total length	0.6226	0.4855
Eye diameter	0.4139	0.2733
Yolk volume	–0.6858	0.4244
BDIP	0.2217	0.4417
BDID	–0.7681	0.2451
BDIA	0.3847	0.3566
Dry weight	0.3887	0.7954
RNA	0.1192	0.5172
DNA	0.4416	0.7385
RNA:DNA	–0.1574	0.0429

Note: Trait abbreviations are as defined in Table 1.

Table 8. Canonical correlation analysis: correlation results between the female canonical correlations and the individual larval traits for the 10 yellow perch maternal lines.

	Canonical correlation	
Larval trait	Female I, driven by female GSI (+) and female egg production (–)	Female II, driven by female size and age (+)
Proportion of variance (%)	54	33.6
Total length	0.5852	0.4410
Eye diameter	0.3891	0.2483
Yolk volume	–0.6446	0.3856
BDIP	0.2804	0.4013
BDID	–0.7220	0.2226
BDIA	0.3616	0.3240
Dry weight	0.3653	0.7226
RNA	0.1120	0.4698
DNA	0.4151	0.6710
RNA:DNA	–0.1480	0.0390

which their eggs are suspended in a matrix of gelatinous material. While it is not clear how reproductive energetic investment is partitioned between the individual eggs and the skein material, it is obvious that as fecundity increases, the quantity of egg skein produced must also increase to accommodate additional eggs. Therefore, the assumption that egg volume is related to GSI cannot be made, and it is likely that differences in yellow perch GSI and egg production do not translate to differences in egg size. We also believe that our lack of data on egg traits partially accounts for the results observed. Had we been able to collect more data on a larger sample size, or on a wider array of the females' egg traits (e.g., dry weight, protein content, nucleic acids content, and lipid content), maternal effects in the egg stage of yellow perch may have been expressed.

Our inability to detect maternal effects in the egg volume or egg yolk volume of yellow perch was not a precursor to a lack of detectable maternal effects in the newly hatched off-

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spring. Differences in the phenotypic traits of the hatchlings from the 10 maternal lines were significantly explained by differences in the phenotypic traits of the females. Previous research on other species has shown that maternal effects were expressed in hatching length, size, yolk sac volume, and oil globule volume (Chambers et al. 1989; Buckley et al. 1991; Chambers and Leggett 1996). Our findings suggest that in yellow perch, maternal effects are expressed most in larval length, yolk sac volume, dry weight, and DNA content. We can ignore the expression of maternal effects in larval body depth at the insertion of the first dorsal fin because this measure is inclusive of the yolk sac and is likely to be driven by yolk sac volume. Also, since the quantity of DNA in a cell is relatively constant within a given species, we expect a higher number of cells in larger larvae than in smaller larvae, and thus a higher quantity of DNA. Therefore, there should be a correlation between larval size and DNA content. Thus, if maternal effects were expressed in one trait, they would be expressed in the other. Near allometric relationships have been shown between larval length and total DNA for capelin, cunner (*Tautogolabrus adspersus*), and radiated shanny (*Ulvaria subbifurcata*) (Pepin et al. 1999); our results provide further evidence for this pattern.

A lack of significant maternal effects in the RNA content and RNA:DNA of the hatchlings from the 10 maternal lines indicates that condition of larvae was not significantly different at hatching. This suggests that differences in protein synthesis may not be exhibited until larvae begin feeding on exogenous food sources, or perhaps until they have utilized much of their endogenous food source. Changes in condition are likely to occur at different rates once the larvae begin depleting their yolk sacs and body reserves and begin first feeding. Such variability in RNA:DNA of first-feeding larvae has been shown for Atlantic herring (*Clupea harengus*) (Clemmensen 1994), Iberian sardine (*Sardina pilchardus*) (Chicharo 1998), and red drum (*Sciaenops ocellatus*) (Rooker et al. 1997).

Female GSI, age, size, and egg production are the key female phenotypic traits that explained differences in the size, yolk sac volume, and DNA content of offspring. Correlation analyses and canonical correlation analyses indicate a potential trade-off between the GSI of the female and her age, size, and egg production. It appears that old, large females with high egg production exhibit low GSI values, whereas younger, smaller females have high GSI values while producing fewer eggs. Ideally, such conclusions would be drawn from a larger sample size of females; however, the depressed Lake Michigan spawning stock was a severe limiting factor in conducting this research. However, despite a small sample size of females, the distribution of female traits used in our experiments was representative of the 1998 adult spawning population in Lake Michigan (Pradeep Hirethota, WDNRFU, Milwaukee, WI 53204, U.S.A., personal communication).

The strong association between larval total length and larval yolk sac volume and female GSI, egg production, and age suggests that it is these female traits that potentially determine the length and amount of yolk a larva may have at hatching. Additionally, the association between female size and age and larval size, as measured mostly by dry weight, and nucleic acid content suggests that it is these female traits that potentially determine the size and amount of nucleic acids of a larva at hatching. On average, older, larger females with high fecundity and low GSI were found to produce offspring that were short with large yolk sacs and high quantities of body reserves, as measured by dry weight and total DNA content. These results suggest that the traits of larvae produced by inexperienced spawners (i.e., spawners of a young age) may be very different from the traits of larvae produced by experienced spawners. While previous studies of maternal effects have not shown trade-offs between larval characteristics that are driven by female characteristics, some correlations have been found. Larval size has been positively correlated with female size (Bernardo 1996), and female size and age have been positively correlated with fecundity (Hislop 1988; Buckley et al. 1991; Chambers and Waiwood 1996).

The correlation between canonical correlation Female 1 and the larval traits from the canonical correlation analysis clearly identifies a trade-off between hatchling total length and larval yolk sac volume. Further, evidence for this trade-off is observed in the box plots for hatchling total length and yolk volume. Across all maternal lines, except Maternal Line 7, those hatchlings with a mean total length greater than the grand mean exhibited mean yolk volumes less than the grand mean, and vice versa. The nonsignificant correlation between larval total length and yolk volume is likely due to the offspring of Maternal Line 7, which exhibited mean total lengths and mean yolk volumes that were greater than the grand means. It is not clear why the offspring of Maternal Line 7 did not exhibit the same pattern as offspring from the other maternal lines. Despite these correlation results, there is a trend in the data suggesting that a negative relationship between larval total length and yolk volume does exist. The trade-off between larval size and yolk volume, when coupled with the strong positive association between larval yolk volume and larval dry weight and DNA content, has potentially substantial implications on the larvae's vulnerability to starvation and predation.

Larger larvae may have an advantage over smaller larvae in that they have been shown to swim faster and thus avoid predators more easily, search greater distances for food, capture larger sizes and quantities of prey, and survive periods of food shortages longer (Miller et al. 1988; Chambers et al. 1989; Chambers and Leggett 1996). However, this does not take into consideration the dangers of initial starvation or the consequences of potential spatial and temporal overlap with prey. Should a larva be faced with a lack of food within a few days of hatching, it will be solely dependent upon its remaining yolk sac and body reserves for survival. Our results indicate that a trade-off exists between larval size and yolk volume that is driven by key characteristics of the female spawning stock. Under circumstances of persistent food limitation after hatching, we would expect smaller larvae with larger yolk sacs and high quantities of body reserves, like those produced by older, larger females, to have a survival advantage over larger larvae with smaller yolks and less body reserves, in terms of starvation. However, assuming that the food limitation is not indefinite, then we would begin to expect the larger larvae to again have a survival advantage over the smaller larvae as feeding and predator avoidance begin to become important. This suggests that po-

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tentially, bigger, as measured by total length, may not necessarily be better in all cases.

Heavily exploited fisheries, especially those that target faster growing, larger females, will be much more susceptible to phenotypic bottlenecking of the female population and subsequently may be at higher risk to recruitment failure when environmental conditions shift. Solemdal (1997) argued that overfishing of the female portion of the spawning stock will cause a population to shift from its fitness peak, since maternal effects are phenotypic. We believe that overfishing of the female portion of the Lake Michigan yellow perch population imposed a phenotypic bottleneck on the population, which was a strong component of the causes of the recruitment failure. The Lake Michigan ecosystem has dramatically changed over the past decade and a half with the introduction of many new exotic species, particularly the zebra mussel (*Dreissena polymorpha*), and it is likely that changes in the environment and high fishing pressure have resulted in stresses on the yellow perch population that contributed to the declines in abundance.

We conclude that the distribution of Lake Michigan yellow perch larval traits at hatching is linked to maternal influences. However, the larval traits that confer a survival advantage likely vary from year to year according to the biotic and abiotic conditions in the lake. The distribution of larval traits artificially selected for through high fishing pressure may not be sufficient for adequate survival and successful recruitment in some years. Therefore, it would be best to manage for a diverse female age and size structure to protect against the inherent environmental uncertainty that exists in nature and to ensure an adequate level of recruitment each year. Managing for diversity of phenotypic traits in commercially valuable species that have declined in abundance is not a new concept. For example, it has been suggested that contributions to sustained annual recruitment of Chesapeake Bay striped bass (*Morone saxatilis*) can result from the maintenance of a diverse female age structure (Secor 2000). No single recruitment mechanism is likely to be responsible for recruitment variation and failure. Rather, a combination of many mechanisms is likely responsible (Leggett and Deblois 1994). However, Solemdal (1997) has argued that because of the complex nature of recruitment mechanisms, maternal effects may be the only recruitment mechanism that can be effectively managed in a fishery through regulation.

Acknowledgements

We would like to thank the Wisconsin Department of Natural Resources Milwaukee Fish Unit and Dan Anderson and his family for all of their efforts in obtaining our yellow perch brood stock. We thank Heather Brussat, Richard and Lori Fulford, Emily Kircher, Chris Ney, and Steve Yeo for their help in the collection and husbandry of the yellow perch and Mary Chenery and Hind Eloukkal for their help in the videotape imaging analysis. We would also like to thank Mary Haasch and Ed Houde for all of their support, enthusiasm, contributions, and efforts throughout this research. We thank Roger Dawson for technical guidance in fluorometric analysis and Bob Anderson for the use of his fluorometer to analyze our nucleic acid samples. We would also like to thank Pierre Pepin for reviewing an earlier draft of this manuscript. This work was funded by the University of Wisconsin Sea Grant Institute under grants from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and the State of Wisconsin. Federal grant No. NA86RG0047, project No. R/LR-75. This is contribution No. 3453 of the University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory.

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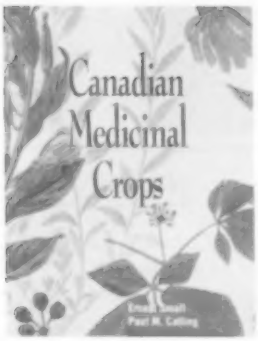

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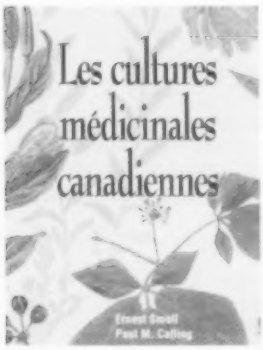

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Canadian Journal of Fisheries and Aquatic Sciences

Volume 58, Number 7, July 2001

Journal canadien des sciences halieutiques et aquatiques

Volume 58, numéro 7, juillet 2001

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0706-652X(200107)58:7;1-4